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ROLF OLIN PETERSON
PURDUE UNIVERSITY

National Park Service Scientific Monograph Series • Number Eleven • 1977

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FOREWORD

In states south of Canada, the once widely distributed gray wolf is represented by two viable populations. The largest inhabits the forested area of northern Minnesota. In this book we are concerned with the second population, which occupies a Michigan island in upper Lake Superior. The wolves of Isle Royale National Park have been intensively studied since June 1958 in a cooperative effort by Purdue University and the National Park Service.

In the first 12 years the work was carried on largely by three graduate students, each of whom produced a doctoral thesis, and two post-doctoral associates on 3-year appointments. It was a fairly long stint as wildlife studies go. The component projects each with its own emphasis, had been tied together nicely by the steadily growing skills of our winter pilot and enthusiastic wolf observer, Donald E. Murray.

By way of initial planning, I had hoped that the program could be maintained for 10-12 years, but by the time Rolf Peterson arrived on the scene, in June 1970, any prospective termination date had receded into the indefinite future. The work of each year confronted our discoveries with new circumstances and new results. There were challenging questions on which we were just beginning to see light.

Rolf was the right man in the right place at the right time. He brought along important assets in addition to his record as a distinguished student in zoology at the University of Minnesota at Duluth. Experience gained on two canoe trips in northern Canada was reassuring; I suspected, correctly, that he could take care of himself. However, there were bonuses of which I was not immediately aware. Rolf had made good in the nationwide fellowship competition of the National Science Foundation. With two renew-

als for which he became eligible, he paid his own stipend for 3 years. In a situation where fund-raising is a never-ending necessity, this was especially welcome. Finally, at the end of the first summer, a bride would enter the program, and it soon became evident that Carolyn Clarke Peterson had much to contribute.

The new phase of the investigation was to be different in several important aspects. The winter of 1969 introduced a series of years characterized by deep snows, abundant runoff waters, and a doubling of the beaver population. Moose and wolves responded with behavior and relationships that were new to us. Wolf increases set the stage for an improved appraisal of territoriality and pack interactions. Above all else, we needed to learn more of the summer habitats of our island wolves. The Petersons as one team, and with two summer assistants as another, literally scoured the island during the warm season. In each of two summers their backpacking exceeded a thousand miles, much of it off-trail, through brush and blowdown, across innumerable swamps and beaver dams. They established contact with the breeding packs and inspected dens and rendezvous sites. They learned to know the island as no one had known it before. After 1970, with everything on the upswing, our "autopsy" file on moose remains examined in the field more than doubled.

The outdoor job was a major demand, but at this stage of the Isle Royale studies we needed a synthesis of findings—the new with the old—that could bring our conclusions reliably down to date. The much-worked-over computer sorting system got more refinements, and Rolf went at it. His thesis produced updated generalizations on 17 years of wolf research.

Appropriately edited, the thesis now appears as number 11 in the Scientific Monograph Series—which replaced and expanded the justly famous National Parks Fauna Series. It tells more than we previously have been able to tell of the island wolves and their prey. It demonstrates how the work on Isle Royale has been well started but by no means finished. As a staff member in biology at Michigan Technological University, Rolf Peterson will employ students, as I have, and go on with the project as its director. We hope the wolves on this island laboratory have a great future and the recording of their history will long continue.

Durward L. Allen
Professor of Wildlife Ecology
Purdue University

27 April 1976

SUMMARY

Predator-prey relationships between timber wolves (*Canis lupus*) and moose (*Alces alces*) were studied from 1970 to 1974 in Isle Royale National Park, a 544-km^2 island in Lake Superior, as part of a continuing research program begun in 1958.

Initial studies in the late 1950s and early 1960s showed that a single large pack of wolves hunted the entire island, preying in midwinter on old adult moose and calves. In nonwinter months wolves relied heavily on moose calves; beaver were a minor food supplement. Moose productivity was very high and was attributed to intensive predation by wolves.

By 1970, moose productivity had declined markedly and there was increased evidence of winter nutritional stress. Young adult moose and calves became especially vulnerable to wolves in winter due to the effects of malnutrition early in life and to the unusually deep snow. Also, wolves relied heavily on an increased beaver population. The food resources for wolves thus were expanded significantly. Concurrently, the size of the original pack's territory was reduced, allowing a second pack to establish itself in the summer of 1971. As a result, the winter wolf population increased from 20 in 1971 to 31 in 1974.

The two principal wolf packs were tracked by plane in midwinter for 234 "pack-days." The packs traveled an average of 11 km/day and 33 km/kill. Travel for both packs was least when, because of snow conditions, moose were easier to kill.

Food availability for pack members ranged from 4.4 kg to 10.0 kg/wolf/day and declined for both packs between 1971 and 1974. Concurrently, the amount of spatial overlap between the two packs increased, leading in 1974 to direct conflict and the death of one wolf.

A social hierarchy existed in both packs, with dominant, or alpha, males and females leading the pack in daily activities. Alpha wolves did most of the mating and discouraged courtship behavior among subordinate wolves. Leadership in both packs exhibited pronounced year-to-year stability.

Wolf predation accounts for most of the adult moose mortality, which occurs primarily in winter. Normally, losses between the ages of 1 and 7 years are relatively light but moose mortality increases steadily thereafter. Average annual adult mortality was estimated by a life-table to be 13%. Male moose die slightly sooner than females and exhibit a higher incidence of arthritis and malnutrition. The oldest males and females recorded were 15.5 and 19.5 years, respectively.

The incidence of moose aged 1–6 years among wolf kills increased from 13% prior to 1970 to 53% since 1970. This reflected a major increase in vulnerability of young moose which appears to have resulted from increased malnutrition early in life and resultant adverse effects on growth and development. Bone measurements revealed that calf size at birth was correlated with the severity of the previous winter, and generations of calves born after winters of nutritional distress account for almost all of the young adult moose killed by wolves.

Increased nutritional stress among Isle Royale moose in the early 1970s apparently resulted from a combination of plant successional trends which reduced browse supply, increased winter severity because of deep snow, and an increase in the moose population during the 1960s.

ACKNOWLEDGMENTS

This study was accomplished only with the help and cooperation of numerous individuals. My wife, Carolyn, served as a field assistant during the nonwinter months and participated in virtually every aspect of the work, from the initial collection of specimens and data to the analysis and, finally, writing and typing of the manuscript. Her enthusiasm for the project and for a relatively primitive life on the island contributed in an important way to the progress of the study.

My major professor, Durward L. Allen, was responsible for initiating the project, and I am grateful for the opportunity to have worked under his direction. His active involvement in environmental issues was a constant source of inspiration, and his advice, criticism, and editorial suggestions were invaluable. I also thank the other members of my graduate committee, Erich Klinghammer, John W. Moser, Jr., and George M. Neher, for their generous contributions of time and assistance. The following individuals read the entire manuscript and offered helpful technical criticism: Anthony B. Bubenik, Mary M. Meagher, and L. David Mech.

The winter work would have been far less meaningful without the experience and guidance provided by Donald E. Murray of Mountain Iron, Minnesota, who has piloted the study aircraft on Isle Royale every year since 1959. His good humor and judgment, in addition to his tremendous aerial tracking ability, were essential ingredients in the annual winter study, and he is responsible for much of the continuity necessary for a long-term project such as this.

Isle Royale Superintendent Hugh P. Beattie deserves special thanks for his constant support and interest, and his permanent and seasonal staff helped in innumerable ways, especially with logistical support and active participation in all aspects of the annual winter study. Fisherman Peter O. Edisen and his late wife, Laura,

residents of Isle Royale for most of their lives, gave unselfishly of their hospitality and help, and their friendship will always be valued highly. Park staff members, researchers from Michigan Technological University, Yale University, and the University of Minnesota, and many park visitors contributed by providing information on the location of moose carcasses and wolf sign.

Former project personnel gathered many records and data used in this study, especially those on moose mortality and herd composition. Their contribution is gratefully acknowledged.

Minnesota pilots Robert R. Mohr, of Crane Lake, the late William J. Martila, Eveleth, and Pat Magie and pilots of Wilderness Wings, Ely, flew moose surveys and winter supply flights safely and efficiently.

The following Purdue University students contributed valuable field assistance during summer: Ronald L. Bell, Timothy C. Lawrence, Joseph M. Scheidler, Philip W. Simpson, John D. Vanada, James D. Woolington, and Michael W. Wrighthouse. Fellow graduate student Fred H. Montague assisted during the winter study in 1972, and James M. Dietz participated in the entire winter study in 1971, when I was on campus, and also served as a summer assistant.

I thank Dr. George B. Rabb for the opportunity to make behavioral observations of a captive wolf pack in Chicago Zoological Garden, Brookfield, Illinois. He and his wife, Mary, were a great help in gaining a working knowledge of wolf behavior that was invaluable in the field. Photographs of Brookfield wolves are used in this publication to illustrate wolf behavior.

Frederick H. Montague made the drawings for the cover and chapter headings. Gerhard C. Peterson drew many of the graphs and maps. All photographs are by the author.

Financial support for Isle Royale wolf and moose studies from 1970 to 1974 was provided by the Boone and Crockett Club, Carnegie Museum, Defenders of Wildlife, National Audubon Society, National Park Service, National Rifle Association, National Science Foundation, and Wildlife Management Institute. Without the support of these government agencies and private organizations, the work would not have been possible.

December 1974

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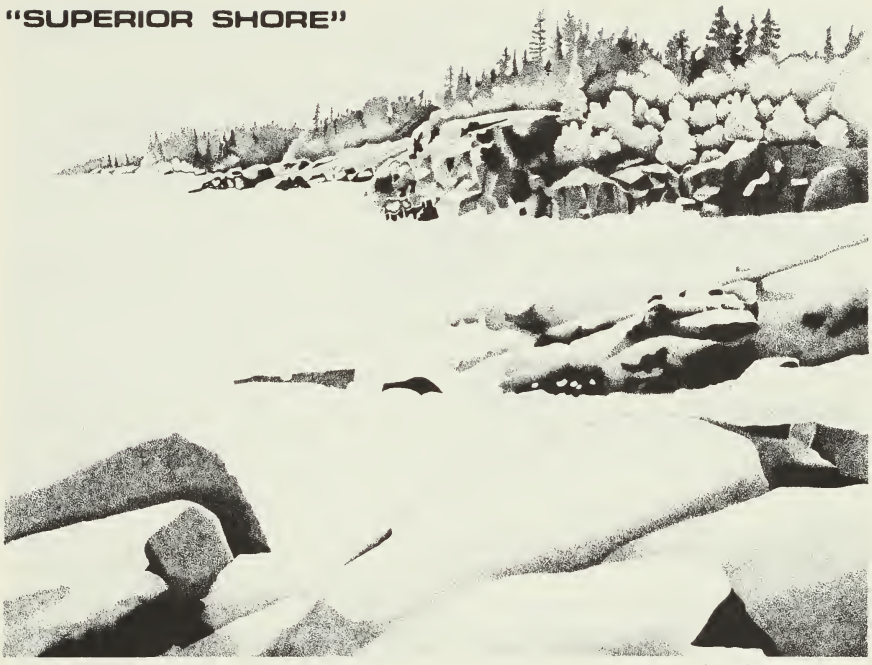


1
Introduction

Opportunities to study the large, native predators of North America in an undisturbed situation are quite rare today, for these animals have been eliminated from most of their former range, at least in the continental United States. Persecution of the gray wolf (*Canis lupus*) has accompanied the spread of modern civilization into every frontier on the continent. Today, wolves are found in the United States only in Alaska, northern Minnesota, and Isle Royale, with perhaps a handful in upper Michigan and in remote areas of the mountainous West. In Canada, wolves still inhabit most of the provinces and territories where the land has not been altered for agriculture or livestock production.

Isle Royale has not always been known for its wolf population. The wolf is a relative newcomer to this island, having arrived in the late 1940s (Fig. 1). For decades prior to their arrival, the island was famous for its moose herd (*Alces alces*), the increase and decline of which attracted nationwide attention (Fig. 2).

Fig. 1. Isle Royale has supported wolves since the late 1940s.

Fig. 2. Moose colonized Isle Royale in the early 1900s.

In addition to concern for the welfare of the moose population, there was great public interest in the other natural features of the island. Although the island had experienced periodic attempts at copper mining and associated disturbances in the form of man-caused fires and logging in the 1800s, by the third decade of this century forest regrowth had restored the landscape. The need to preserve this unique island was clear by the late 1920s, and Isle Royale was established as a national park in 1940.

The island has been the focus of many geological, botanical, zoological, and archaeological studies since the early part of this century. After wolves colonized the island, biologists were presented with a predator-prey system uncomplicated by a great number of interacting species and, importantly, an ecosystem set aside by man for preservation of its natural features.

A long-term study of wolf-moose relationships on Isle Royale began in 1958 under the direction of Durward L. Allen of Purdue University. Individuals with principal responsibility for field studies in wolf-moose ecology were L. David Mech, 1958–62; Philip C. Shelton, 1962–63; Peter A. Jordan, 1964–66; and Michael L. Wolfe, 1967–70. My work began in 1970.

In this monograph, previous published work on the Isle Royale wolves is briefly reviewed. Data gathered on the wolf population from 1971 through 1974 are presented in detail. I also have attempted a synthesis of moose mortality data recorded in systematic fashion from 1958 through the winter study of 1974 to provide a composite picture of mortality patterns.

Study Area

Isle Royale is actually an archipelago, distinguished by a single large island 72 km long and 14 km at the widest point. Many small islands extend off the peninsulas of the main island. The closest Canadian island is 20 km from Isle Royale, and the Canadian mainland is 24 km distant. Although Isle Royale is part of Michigan, it is closer to the northeastern tip of Minnesota (Figs. 3, 4).

Geology and Physiography

Recent geological investigations of Isle Royale (Huber 1973a, b, c; Wolff and Huber 1973) provided the basis for this brief account of the formation and subsequent reworking of the bedrock strata that form this island.

The oldest rocks found on Isle Royale are Keweenawan lavas, which probably erupted a little over a billion years ago from what is now the middle of the Lake Superior basin. Occasionally, sedimentary deposits washed in from surrounding regions as the areas slowly subsided, resulting in interbedded volcanic and less-resistant sedimentary strata. Continued subsidence created the basin which now contains Lake Superior and tilted the bedrock strata that form Isle Royale toward the southeast (Fig. 5).

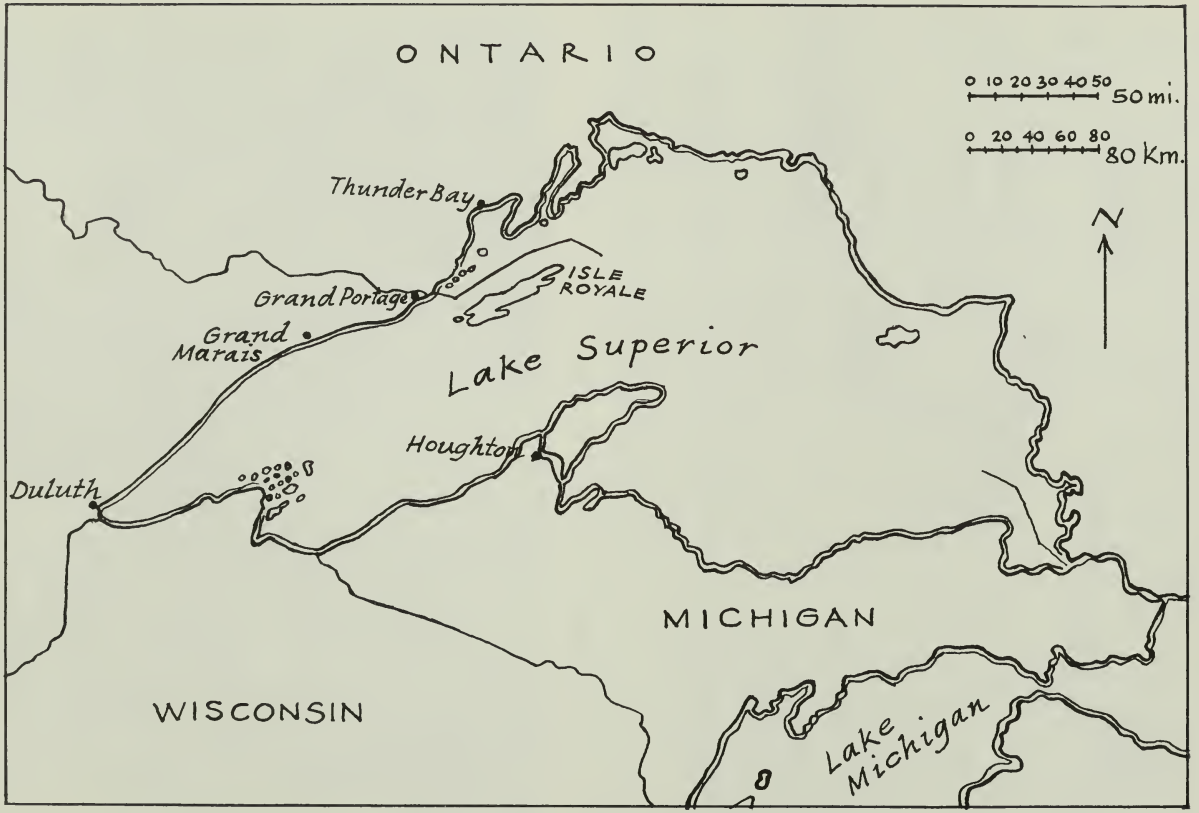


Fig. 3. Map showing location of Isle Royale.

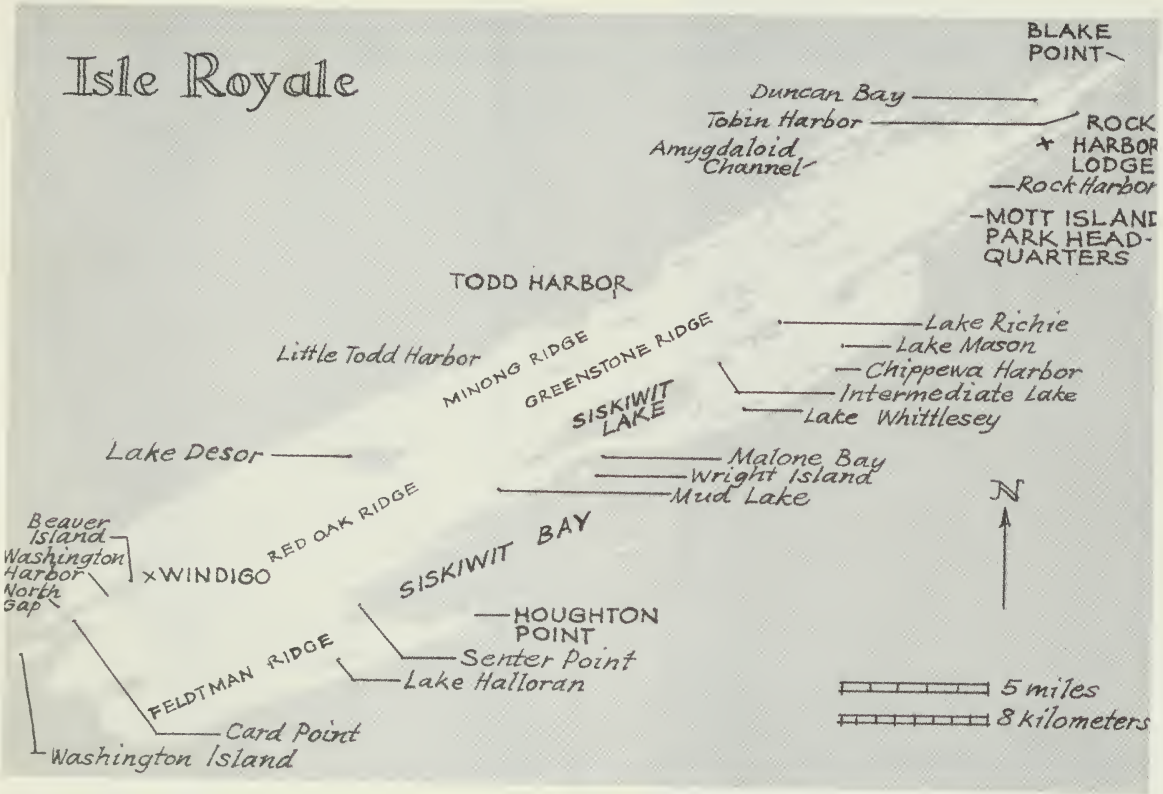


Fig. 4. Map of Isle Royale, showing locations mentioned in text.

Preglacial stream erosion removed portions of the softer strata running the length of present-day Isle Royale. Glacial ice further scoured these valleys, resulting in the longitudinal ridge-and-valley topography that is characteristic of Isle Royale (Fig. 6). The final glacial retreat occurred during the Valderan period, about 11,000 years ago. The ice withdrew in a northeasterly direction, exposing the western end of the island first, then halted for a period of time just west of Lake Desor. Consequently, significant deposits of glacial debris can now be found at the southwestern end of the island, while the more rapid retreat of ice from the northeastern end left little material behind. Further retreats of the glacier opened up successively lower outlets for the large, postglacial lakes that formed at the edge of the ice, and lake levels dropped, exposing more of Isle Royale. Coupled with the fall of lake levels has been a slow postglacial rise of the bedrock. The highest elevation on the island is 238 m above Lake Superior, which lies 181 m above sea level.

The soil mantling the northeastern two-thirds of the island is, for the most part, thin and azonal, with many sloping ridges devoid of soil except in depressions. Exposure of bedrock on the southwestern third of the island is much less frequent, and soils are somewhat deeper and more developed, primarily because glacial deposits at this end were greater.

Climate

Surrounded by the world's largest body of fresh water, Isle Royale's climate is greatly modified relative to nearby mainland areas. The principal effects of Lake

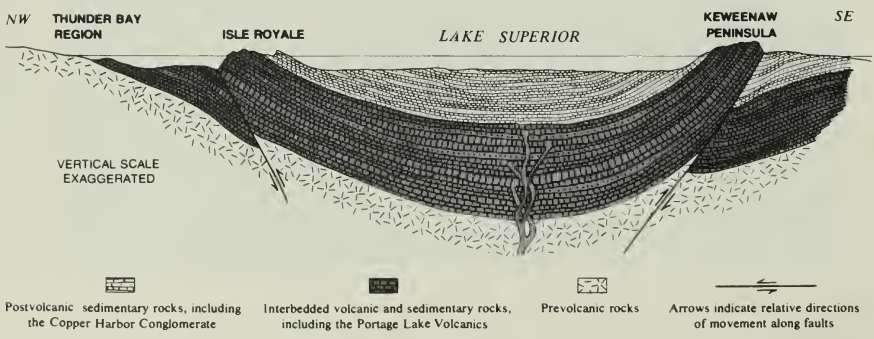


Fig. 5. Cross-section through Lake Superior, Isle Royale, and Keweenaw Peninsula (Huber 1975).

Fig. 6. Characteristic ridge and valley topography of Isle Royale.

Superior are to buffer temperature changes and increase precipitation and humidity over the island (Fig. 7).

TEMPERATURE

Isle Royale temperatures are generally cooler in summer and warmer in winter than those of the mainland, with less range in temperature extremes. Temperatures of −34°C (−30°F) have been recorded only three times in the last 14 years, with the record −37°C (−35°F) recorded in 1972. The mean number of days per year with a maximum temperature over 32°C (90°F) is only two along the north shore of Lake Superior (U.S. Department of Commerce 1968); however, further inland in Minnesota, extreme temperatures over 32°C and below −34°C are not uncommon.

Temperatuers during the annual 7-week winter study are generally above −18°C (0°F) (Fig. 8), and thaws in midwinter are frequent. The years 1964 and 1973 stand out as unusually warm, while 1967 and 1972 were, on the average, the coldest recorded since measurements began in 1962.

PRECIPITATION

Most of the weather systems that move over Isle Royale come from the northwest, and moisture is picked up as they cross Lake Superior. Those storms

Fig. 7. Lake Superior is responsible for high humidity and frequent fog.

which do come from the east bring more moisture toward Isle Royale and the Minnesota shore of Lake Superior. Precipitation in northeastern Minnesota, closest to Lake Superior, is considerably above that of northwestern Minnesota. Precipitation on the south side of the lake, in upper Michigan, is even greater, since this area receives moisture picked up by prevailing winds (Table 1). Annual precipitation for Isle Royale has not been measured on a year-round basis but is probably intermediate between northeastern Minnesota and upper Michigan.

Snowfall. Mean annual snowfall on the north shore of Lake Superior (1931–60) was approximately 150 cm, while the Keweenaw Peninsula in upper Michigan received in excess of 250 cm. The average snowfall for Houghton, Michigan, was 452 cm from 1931 to 1960 (U.S. Department of Commerce 1968). In recent years, when water content of snow was measured on Isle Royale during the annual study period, precipitation (ca. January–March) on the island was 55–60% more than the nearest mainland stations in Minnesota, and about 40% less than Houghton, Michigan, on the south side of the lake (Table 2).

Peek (1971a), working in northeastern Minnesota, found that snow depths were greater and crusts stronger in the part of his study area closest to Lake Superior. On Isle Royale, mild temperatures may produce crusting conditions that do not exist in colder, mainland areas. In all three winters that I have spent on the island, there were well-developed crusts either within or on top of the snowpack for a sufficient length of time to affect either wolf mobility or moose habitat preference.

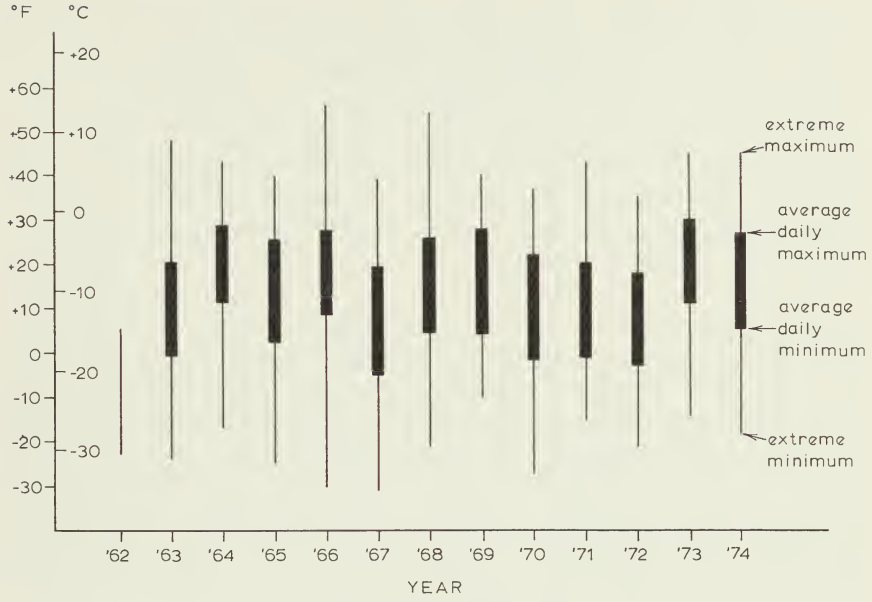


Fig. 8. Winter temperature records for Windigo, Isle Royale National Park.

TABLE 1. Mean annual precipitation in mainland areas in Minnesota and Michigan (1931–55).[a]

	cm	Millions of liters/ha
Northwestern Minn.	53.3	5.4
Northcentral Minn.	62.5	6.3
Northeastern Minn.	69.3	7.0
Western half, Upper Peninsula, Mich.	82.0	8.3

[a]U.S. Department of Commerce, 1968.

During the span of wolf-moose studies on Isle Royale, trends in snowfall and snow depth have been generally upward, though not without great year-to-year

TABLE 2. Winter precipitation (cm) on Isle Royale and nearby mainland weather stations.

	Total Precipitation			
	1972 19 Feb.–10 Mar. (21 days)	1973 27 Jan.–14 Mar. (47 days)	1974 23 Jan.–16 Mar. (53 days)	Station total (121 days)
Grand Marais, Minn.[a]	2.67	4.65	4.06	11.38
Grand Portage, Minn.[a]	2.87	5.66	2.36	10.89
Windigo, Isle Royale	3.30	8.26	6.05	17.61
Houghton, Mich.[a]	9.80	10.54	9.35	29.69

[a]U.S. Department of Commerce 1972–74.

variation. Measurements of snow depth on Isle Royale during the winter period have not been taken consistently, so Grand Marais weather data were used to show trends. These data indicate above-average snow depths for the mid-1960s and for 1969 through 1972 (Fig. 9). A snow-depth index was plotted for this station, utilizing maximum depths recorded in each month from November through May. These depths were used to construct a graph of maximum snow depths for each winter since 1958–59 (Appendix A). The area under the curve was determined using a grid overlay (Bishop and Rausch 1974). While not corresponding precisely to conditions on Isle Royale, this index can be used to indicate year-to-year variations in snow depth.

Isle Royale snow studies. In addition to snow depth, other physical characteristics of snow were measured to interpret more adequately the effects of snow on moose and wolf mobility and behavior. The support quality of the snow was measured in 1972 and 1973 with a compaction gauge similar to that developed by Verme (1968), and in 1974 with a Swiss Rammsonde penetrometer. The Ram penetrometer gave more satisfactory results when crusts were present on or near the snow surface. Both instruments rely on vertical force to penetrate the snowpack although they differ somewhat in design and use (Appendix B). Snow depths and penetrability readings were taken frequently at three sites differing in canopy coverage. Density and hardness within the snow profile were measured from one to three times during each winter study according to the method of Klein et al. (1950).

Snow depths varied considerably according to the type of overhead canopy and exposure to the wind, and were greatest in open areas and least under thick conifer canopies. Snow depths in an open area protected from the wind were consistently at least 20–25 cm greater than a nearby site beneath a thick canopy (Fig. 10).

Overhead canopy also affects maturation of the snow. The effects of sun and wind, principally responsible for the formation of crusts and settling of snow, are reduced considerably by a dense overhead canopy. Usually, crusts beneath conifer canopies are less well developed, and vertical hardness is almost always lower in canopied areas (Kelsall and Prescott 1971:134–137). The support quality of such snow, of course, is considerably less (Figs. 11 and 12).

An important exception to the general rule of softer snow beneath conifers occurs during thaws, when snow remaining on conifer canopies (called "qali", Pruitt 1958) melts and drips onto the snow surface below. This occurred in early March 1973 and 1974, resulting in a strong surface crust and increased snow density over the entire island, especially below conifers. Crust strength in these situations was quite variable throughout the day, depending on the temperature.

A small number of snow profiles were studied by digging a pit to ground level. Physical characteristics of each distinct layer of snow were recorded. These snow-profile analyses revealed that the density of fresh snow on Isle Royale was usually between 0.06 and 0.10 g/cm^3, and as the snow matured, its density increased accordingly. Density of well-aged snow on Isle Royale ranged from 0.30 to 0.35 g/cm^3. These changes in snow density are evident in the top layers of the snow profiles shown in Appendix C.

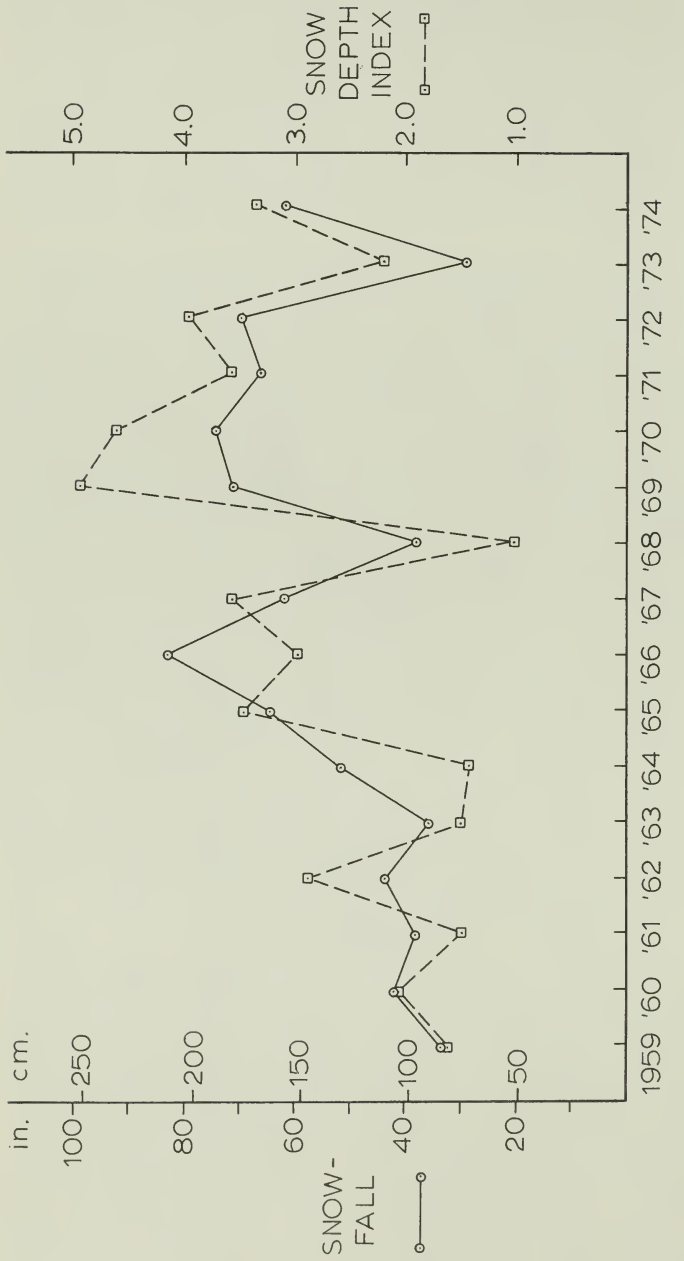


Fig. 9. Snowfall and index of snow depth at Grand Marais, Minnesota, 1959-74.

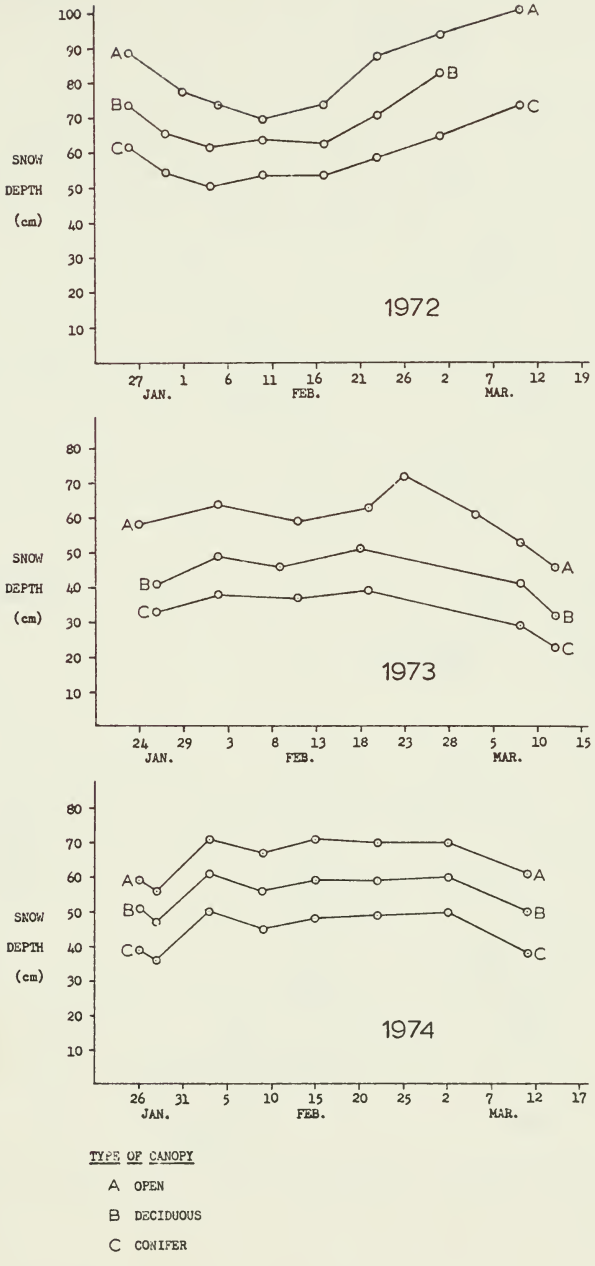


Fig. 10. Snow depth at three sites on Isle Royale, 1972-74, illustrating annual variations in snow levels and the effect of overhead canopy.

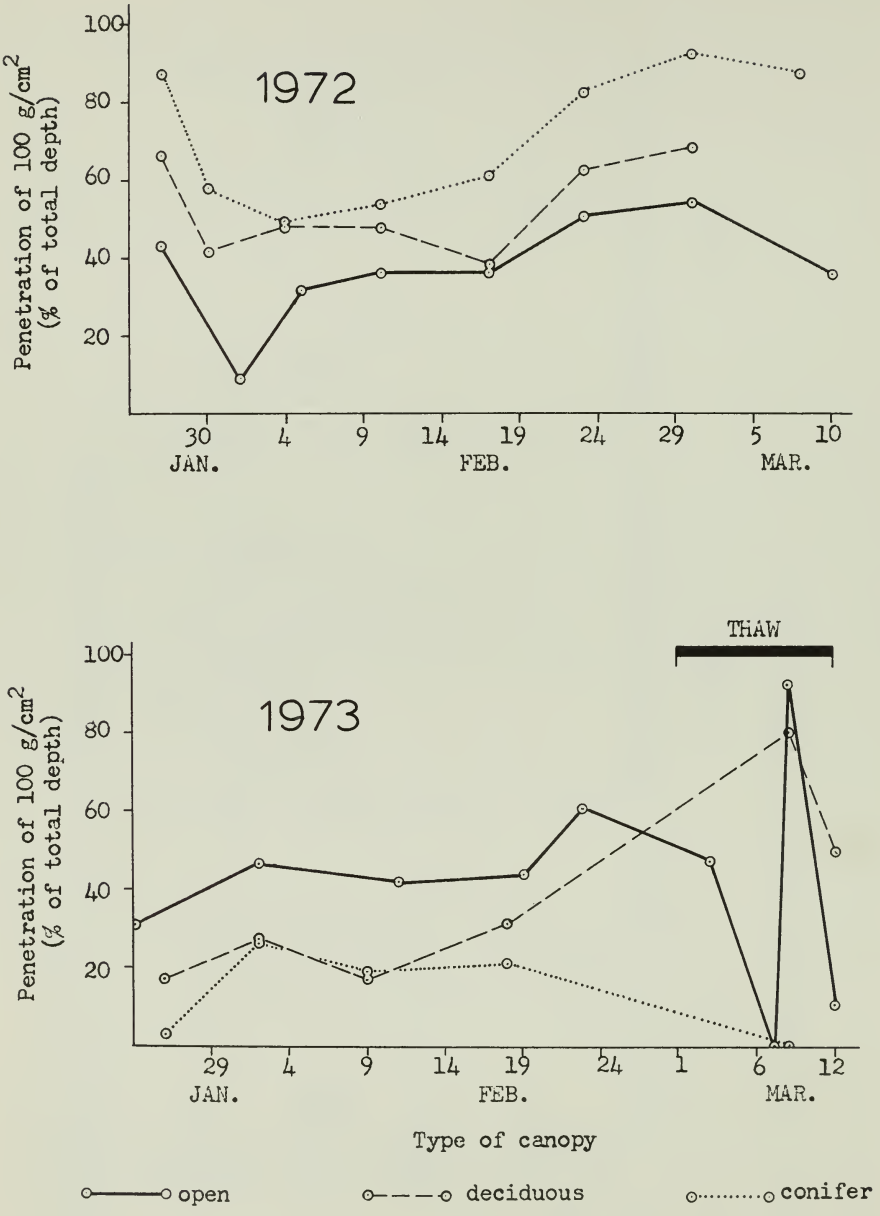


Fig. 11. Penetrability (determined by compaction gauge) of snow at three sites on Isle Royale, 1972-73.

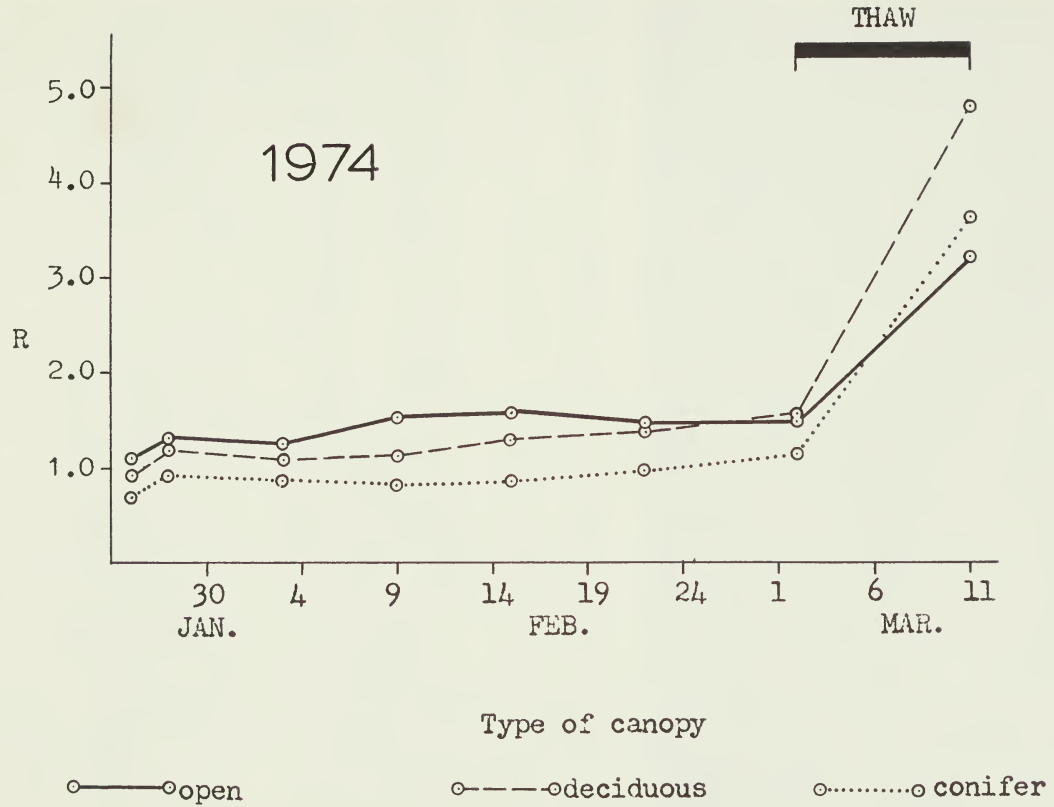


Fig. 12. Ram hardness number (R) (Appendix B) of snow at three sites on Isle Royale, 1974.

Vegetation

Isle Royale is almost entirely forested. Fire history, glacial deposits, and a "washboard" topography all contribute to a rich mosaic of tree species. Because the island lies in a transition zone between the boreal and the northern hardwood forests, elements of both grow here. Typical boreal tree species are found near the Lake Superior shoreline, where atmospheric moisture is greater and temperatures during the growing season are lower and less variable than further inland (Linn 1957). These include white spruce (*Picea glauca*), balsam fir (*Abies balsamea*), white birch (*Betula papyrifera*), and aspen (*Populus tremuloides*). Coniferous vegetation normally succeeds deciduous species in this forest type, leading to extensive stands of spruce and fir (Fig. 13).

At higher elevations in the interior of the island, the principal tree species are sugar maple (*Acer saccharum*) and yellow birch (*Betula allegheniensis*), common elements of the northern hardwood forest (Fig. 14). In areas between the two principal climax types, Linn (1957) found hardwoods dominant on dryer sites and conifers dominant wherever soil moisture was sufficient for their existence.

Hansen et al. (1973) described stand composition in detail for the principal forest types found on Isle Royale. Krefting et al. (1970) delineated these in a vegetation map (Fig. 15).

The forest designated as aspen-birch-fir-spruce is typically composed of old-growth, deciduous stands with ample coniferous reproduction. Spruce and fir dominate such stands, particularly at the northeast end. This forest type, usually found along the lakeshores of the island, now provides the most important winter habitat for moose on the island.

Areas designated as aspen-birch are also old-growth stands that emerged after fires in the previous century. Coniferous reproduction is relatively sparse both here and in sugar maple-yellow birch stands.

About 20% of the island (10,400 ha) burned in 1936; 576 ha within the 1936 burn, south of Lake Desor, burned again in 1948 (Krefting 1974). Regeneration, mainly aspen and birch, followed these burns, although today there are many other species resulting from different intensities of burn and perhaps remaining seed sources (Fig. 16). Cedar (*Thuja occidentalis*) is common within areas of the 1936 burn in lowlands west of Siskiwit Bay. In the center of the island, solid stands of aspen and birch now have grown out of reach of moose, and there is little coniferous reproduction. White spruce is common in the 1936 burn east and south of Lake Richie, with stands interspersed with large areas of bare rock outcrops.

Mammalian Fauna

Isle Royale is sufficiently far from the mainland to isolate it effectively from colonization by many terrestrial species. Sixteen species of mammals occur presently on Isle Royale (Table 3); Johnsson and Shelton (1960) list an additional 30 mainland mammals that have never been recorded on the island (Figs. 17, 18, 19). Coyotes (*Canis latrans*) and woodland caribou (*Rangifer tarandus*) inhabited

Fig. 13. Spruce-fir forest is typical of Isle Royale shorelines.

the island within the current century but are not present now. The Norway rat (*Rattus norvegicus*) and white-tailed deer (*Odocoileus virginianus*) were introduced but did not persist on the island. The long-tailed weasel (*Mustela frenata*) and red-backed vole (*Clethrionomys gapperi*) were recorded on the island in the early 1900s, but Johnsson and Shelton (1960) considered these records doubtful. Marten (*Martes americana*) were also said to occur in the early 1900s, but evidence is sparse.

Of the four bat species listed for the island, I identified only the little brown bat (*Myotis lucifugus*) between 1970 and 1974. Johnson and Coble (1967) found positive evidence of the red bat (*Lasiurus borealis*) in castings of pigeon hawks in 1966, providing the only island record for this species. Of the remaining 12 species of mammals, I observed all but the lynx (*Lynx canadensis*) and short-tailed weasel (*Mustela erminea*). Weasel tracks were seen each winter from 1971 to 1974. A cat, judged by its tracks to be a lynx, was seen by Donald E. Murray and Ranger Zeb McKinney in winter 1970 (Murray, pers. comm.). If lynx are still present on the island, they are very rare.

The status of the otter (*Lutra canadensis*) was uncertain in the early 1960s (Mech 1966), but well-distributed signs of otter were seen regularly each winter 1972–74. This species appears to be a recent colonizer of Isle Royale that has increased steadily.

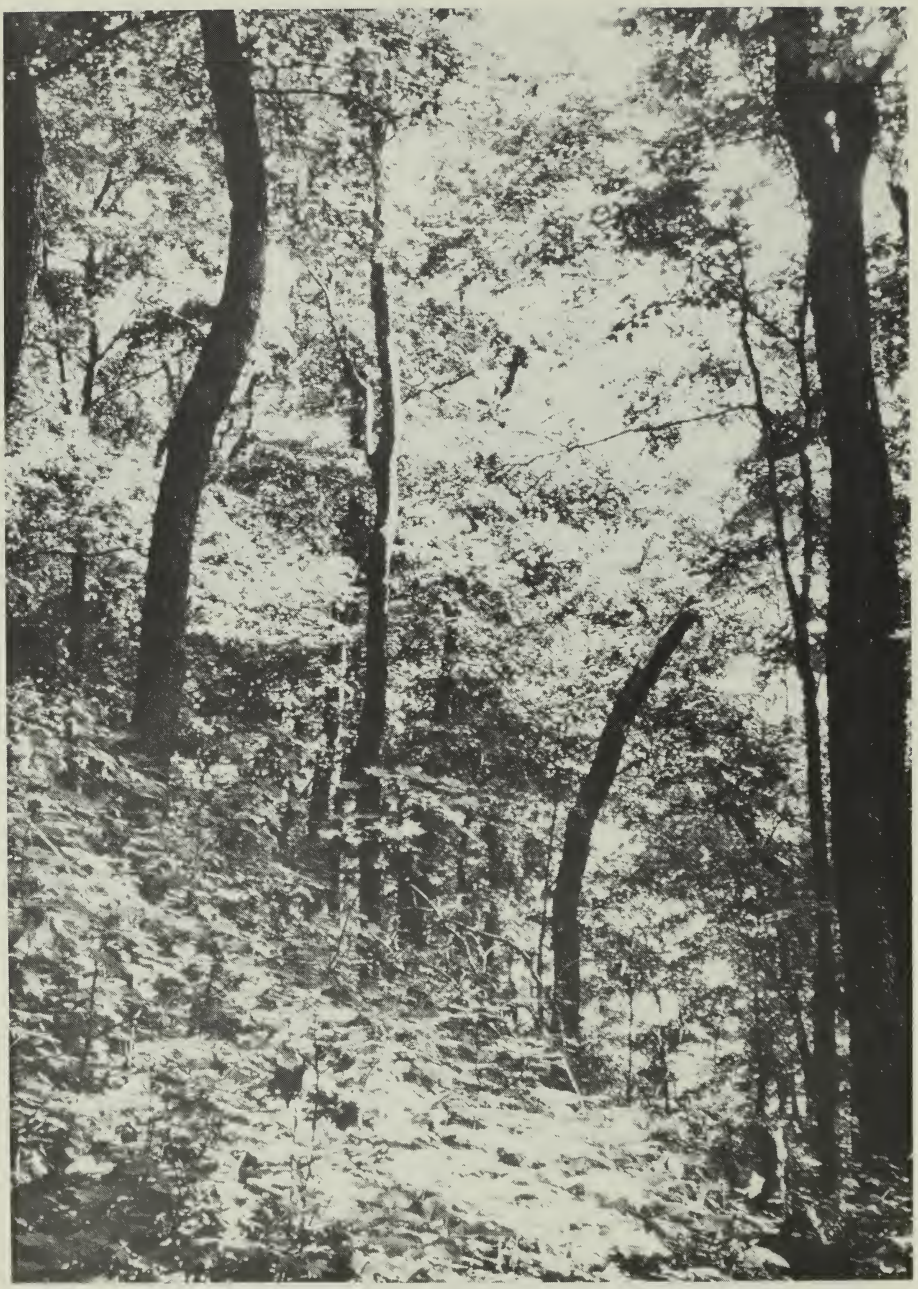


Fig. 14. Yellow birch—sugar maple forest in island's interior.

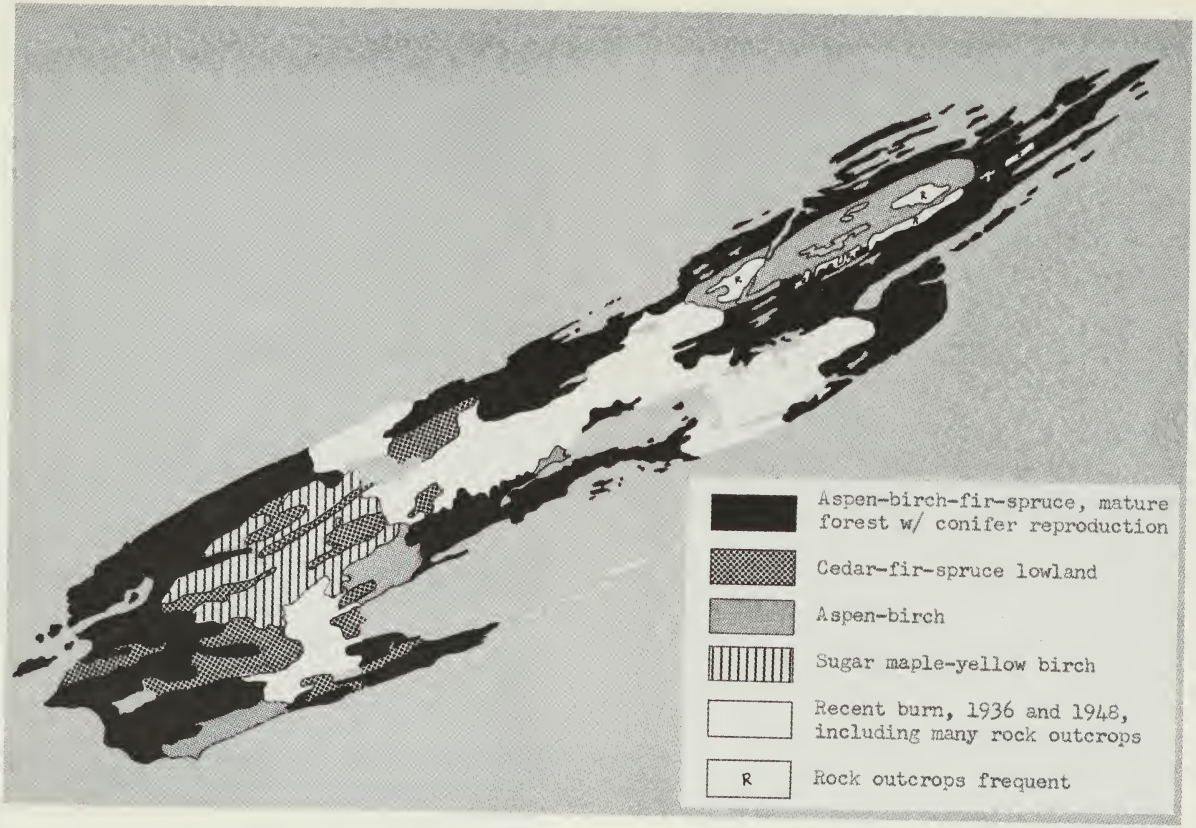


Fig. 15. Vegetation map for Isle Royale, modified principally from Krefting et al. 1970.

Fig. 16. Fires and subsequent erosion create thin soils on ridgetops.

TABLE 3. Mammals currently present on Isle Royale.

Gray wolf	*Canis lupus*
Red fox	*Vulpes vulpes*
Short-tailed weasel	*Mustela erminea*
Mink	*Mustela vison*
Otter	*Lutra canadensis*
Lynx	*Lynx canadensis*
Moose	*Alces alces*
Snowshoe hare	*Lepus americana*
Red squirrel	*Tamiasciurus hudsonicus*
Beaver	*Castor canadensis*
Muskrat	*Ondatra zibenthicus*
Deermouse	*Peromyscus maniculatus*
Little brown bat	*Myotis lucifugus*
Keen myotis	*Myotis keenii*
Big brown bat	*Eptesicus fuscus*
Red bat	*Lasiurus borealis*

Fig. 17. Woodland deermouse, the smallest rodent species on Isle Royale.

Fig. 18. Snowshoe hare, primary prey of the red fox on Isle Royale.

Fig. 19. A unique subspecies of red squirrel inhabits Isle Royale.

Fig. 20. Pilot Donald E. Murray.

Methods of Study

Field work was concentrated in two periods: 7 weeks in midwinter and roughly 6 months from May to October (Appendix D). While field techniques varied seasonally, the emphasis at all times centered about increasing our knowledge of wolves and wolf-moose relationships on Isle Royale. Wolf study methods were basically observational, with heavy reliance on aerial tracking in winter and reading wolf sign in both summer and winter (Fig. 20). Carcasses and skeletons of moose were examined whenever possible. Size and composition of the moose population were estimated by aerial methods.

Winter Wolf Study

The winter study extended from late January into mid-March, which is normally the period when ice in the harbors and lakes is sufficient to land a ski-plane. Headquarters for the annual winter study were at Windigo, at the southwest end of the island. Knowledge of wolf movements came only from aerial tracking. Shorelines of the island and inland lakes (preferred wolf travel routes) were followed from the air whenever possible to locate wolf tracks. We tried to maintain a complete travel record for the main packs by backtracking to the location of the previous observation. Small groups and single wolves were located whenever possible by checking old kills of the large packs.

When time permitted, we circled wolves at an elevation of several hundred feet and observed them with binoculars, recording data on a portable tape recorder. From 1972 through 1974, I observed wolves from the air for 30 hours. Ground observations were possible at carcasses of necropsied moose at Windigo. Identification of individual wolves was based on body markings; the relative fullness of the tail and variations in the dorsal spot and tip of the tail were the most useful characteristics. The number of individual wolves identified varied from year to year and depended on the distinctiveness of wolf body markings and the amount of time available for observation. Usually, identification from one day to the next, and especially from one year to the next, was limited to the alpha or dominant male and female in each pack. Photographs proved helpful in year-to-year identification of alpha wolves.

Captive wolves were observed at the Chicago Zoological Garden, Brookfield, Illinois, to aid interpretations of wolf behavior in the wild. Behavior patterns were the sole means of sex determination for Isle Royale wolves. Both males and females often exhibit the same or only slightly different behavior, so one must be cautious when drawing conclusions. For example, while males may lift a hind leg when urinating, females occasionally do likewise. The only urination posture that is unambiguous is the male's leaning forward, with back legs outstretched (Fig. 21). If the anal region of a wolf is examined frequently by other wolves during the breeding season, it is safe to assume that the animal examined is a female. The examining wolf is not necessarily a male however, since female pups at Brookfield

Zoo exhibited the same behavior. In each pack, the dominant, or alpha, male and female were distinguished by the fact that they never displayed submissive behavior toward other wolves, while other wolves were submissive in their presence.

Identification of pups in midwinter presented a problem. Sometimes pups could be distinguished by their behavior. Pups seemed to be more playful, were sometimes hesitant in situations such as crossing glare ice, and behaved inconsistently toward dominant wolves during group greetings. Sometimes pups were distinguished by a lighter, uniform color, slim body, and guard hairs that stick up along their back, creating a scraggly outline (Fig. 22). At other times, however, pups and adults are indistinguishable. For example, in 1974 we examined the carcass of a wolf that appeared to be an adult. Unworn canine teeth and lack of epiphyseal closure in the radius (Rausch 1961), however, showed that it was actually a pup. Underdeveloped pups may be more pup-like in appearance (Van Ballenberghe and Mech 1975), leading one to conclude that pups are plentiful and show high survival in years when actually they were identified only because they were underdeveloped. Thus, the number of pups distinguished by appearance and/or behavior could not be used as an annual index to pup production and survival.

Fig. 21. East Pack alpha male (1974) urinating in posture unique to males; alpha female stands behind him.

Winter Moose Census

The present phase of the Isle Royale studies was initiated in 1970 with a firm foundation of aerial moose-inventory techniques which have been steadily refined. The first aerial censuses on Isle Royale used a transect, or strip, method, in which all the moose seen in midwinter during many parallel flight lines were tallied (Aldous and Krefting 1946) (Fig. 23). Cole (1957) and Mech (1966) employed a variation of this strip method by "buzzing" moose that were spotted in order to flush any nearby animals. Mech's 1960 census was the last attempt at a complete count of the Isle Royale herd. Weather factors and moose-distribution patterns in subsequent years were such that stripwise coverage of the island would have produced a far less meaningful estimate. In addition, confidence intervals cannot be constructed for such an inventory.

Although Jordan (unpubl. data) employed a strip census method in 1964, it was discontinued thereafter in favor of intensive aerial searching of small plots randomly distributed over the island. After 1965, the island was divided into several zones of relative moose densities. The plots occurring in each zone were used to calculate mean moose density and variance for that zone (Wolfe and Jordan, unpubl. data).

I used a similar aerial-plot method. Since the population estimate depends on the area included in each zone of moose density, it is important that the zone assignments accurately reflect current moose distribution. For this reason I made some modifications in zones in both 1972 and 1974.

Winter moose censuses in both years were flown in a 90-hp Aeronca Champion. We flew overlapping circles a few hundred yards wide over a given plot until it had been covered completely. Most plots were flown at an altitude of 100-200 m; the "open" character of burned-over areas permitted a censusing altitude of about 250 m. Moose densities were highest in coniferous cover where visibility was poor, so these areas were circled most intensively. Counting in both years continued throughout February. Although the counting period was long, no noticeable variations in moose distribution invalidated the zone assignments. Within each zone, we attempted to sample plots randomly, but in practice this plan was modified considerably by the weather and a need to minimize time spent flying from one plot to another. Plots were counted in areas where flying and counting conditions were near optimum: little or no wind (less than 10 mph), and a high overcast to eliminate shadows. Allocation of sampling among the zones was such that sampling error would be minimized at whatever point the work was terminated. Censusing in both years was discontinued early in March after moose were confined to areas of conifer cover by strong crusts on the snow surface.

ACCURACY OF AERIAL MOOSE CENSUS

Studies in Alaska show that observer experience, number of observers, snow conditions, time of day, terrain, and type of aircraft could all affect moose counts

Fig. 22. Pups may appear scraggly, as three wolves on left, or may be indistinguishable from adults.

Fig. 23. Aerial counts were used to determine moose population size and composition.

Fig. 24. Summer field headquarters on Rock Harbor.

(LeResche 1970; LeResche and Davis 1971; LeResche and Rausch 1974). Inexperienced observers saw less than half of the moose in experimental enclosures, even under good conditions. In nine counts by an experienced observer, with the pilot participating, the average proportion of moose seen was 70%; the highest accuracy attained in such a count was 87%. The flight patterns were either narrow transect or concentric circles of ever-decreasing radii.

Compared to the relatively open cover of the Alaska study area, Isle Royale has large areas of dense conifer cover which make moose counting more difficult. In addition, moose concentrate in these conifer areas, further reducing accuracy. To compensate somewhat, we spent a greater amount of time circling each plot. The Isle Royale plots were kept small (1–2 km^2) to reduce observer fatigue and resultant errors.

An accuracy of 80% was assumed for the 1972 and 1974 counts. Factors responsible for the assumed high level of accuracy are the flight pattern of overlapping circles, the intense circling, and the long experience of the pilot.

Aerial moose counts probably can do little more than provide a rough index of trends in the population. In addition to the above problems, the uneven nature of moose distribution contributes to a high sampling error; 95% confidence intervals are generally in excess of 20% of the estimate (Evans et al. 1966; Mantle 1972:124–137; Peek 1971a).

Summer Ecology of the Wolf

Most of the spring-fall field work consisted of ground searches for moose remains and wolf sign (Fig. 24). Since wolves made extensive use of the 270 km of hiking trails during spring and fall, when visitation is lowest, we also walked the trails at these times, monitoring wolf sign and checking for the occasional kill made on a trail. When human activity caused the wolves to abandon the trails, we generally did likewise. Open ridges, shorelines, creek beds, swamp edges, and animal trails then became our travel routes.

Howling responses were sometimes useful in locating wolves. Human imitations of howls were frequently broadcast over the island in 1971 and 1972 through a portable megaphone with electronic amplification. However, success was limited because we could move about only on foot. By checking known travel routes and reports of howling, we finally located wolf activity areas (den and rendezvous sites) in the summer of 1973. The presence of wolves at summer homesites was then monitored by camping near enough to hear spontaneous howling. In order to minimize disturbance to the wolves, human howling was employed to elicit wolf responses only when the location of wolves was uncertain.

We collected a large sample of wolf droppings (scats) in summer 1973, to determine food habits at this time of year. All samples were autoclaved to avoid contamination by *Echinococcus,* a tapeworm whose eggs are passed with feces. Scats were pulled apart under a binocular scope, and the incidence of prey remains

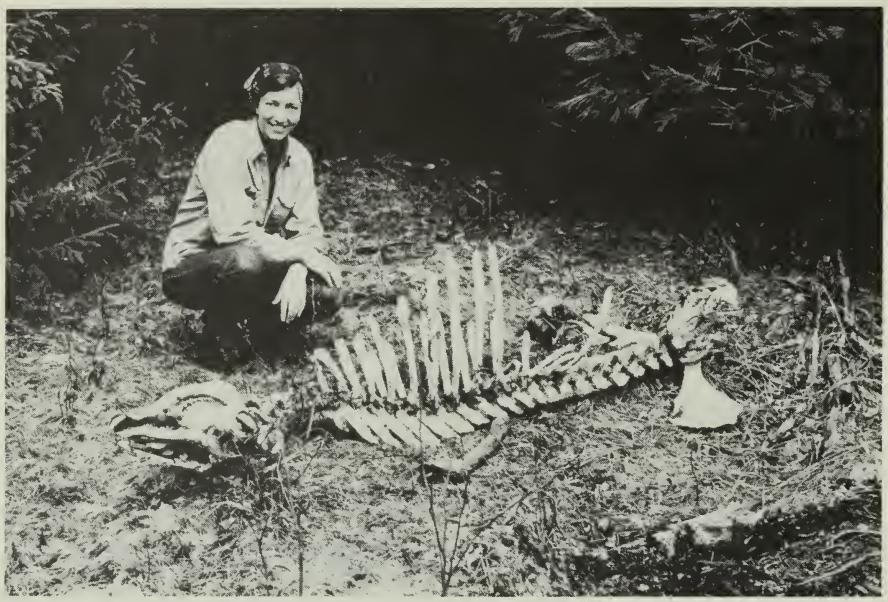


Fig. 25. Extensive carcass examinations revealed moose mortality patterns.

in each scat recorded. Hair was examined under reflected light and magnification. Identification was aided by photographs and descriptions provided by Adorjan and Kolenosky (1969).

Moose Mortality Patterns

The collection of skeletal remains of Isle Royale moose over a 16-year period (1958–74) provided a unique opportunity to investigate mortality patterns in a naturally regulated moose herd and to document changes in the type of moose killed by wolves from one year to the next. In addition to the winter-spotted kills, other carcasses and skeletal remains located at random during summer field work provided data on year-round mortality (Fig. 25). Information on date and cause of death, age, sex, skeletal abnormalities, and marrow condition was recorded whenever possible.

Since 1959, a major effort has been made each winter to locate wolf kills, primarily by following wolf tracks. Sometimes this has led to carcasses of old kills or moose that died of causes other than wolf predation. Almost all of these dead moose were subsequently ground-checked, either in winter or as soon as possible the following spring. Of 141 carcasses located in winter (1971–74), 136 were examined from the ground. An additional 292 carcasses or skeletal remains were examined in summer (1970–73).

The autopsy record file was the primary source of material for the discussion of mortality patterns. Information from the entire collection (836 known-age moose) was reviewed and coded to utilize computer-sorting. During the most recent phase of the project (1970–74), age was determined for 404 moose (of the 428 remains examined).

An approximate date of death was assigned to each dead moose according to the degree of decomposition or weathering. The presence of hair, rumen contents, hide, and various decomposing organisms indicated death within a year, usually the previous winter. Bits of dried flesh rarely persist for more than 2 years, especially in wet sites where decomposition proceeds at a more rapid rate. Bones often remain on the ground on Isle Royale for a decade or more, since none of the rodent species on the island gnaw bones other than antlers to any great extent, and weathering is very gradual (Fig. 26). Remains older than 2 years were placed in one of three groups: 2–5 years, 5–10 years, or more than 10 years, and in most cases an approximate 5-year period covering the estimated time of death; e.g. 1960–64, 1965–69, 1970–74. Since I often found bones from moose that had been examined by project personnel in previous years, there was ample opportunity to check this method of estimating time of death against old remains with a known date of death.

When possible, a cause of death was assigned. Bones that were heavily chewed and widely scattered indicated that wolves had fed on the carcass. Such remains were classed as probable wolf kills because winter observations indicated that wolves on Isle Royale killed most of the moose upon which they later fed.

Calves were aged according to tooth eruption criteria; all adults were aged by counting cementum annuli in a section of polished upper or lower molar. Wolfe (1969) believed that a conservative estimate of the reliability of this technique would be ± 2 years. But, if cementum annulations are consistent and clearly visible, accuracy is much improved (Fig. 27). I have found some variation in the clarity of annulations in a few specimens; for such moose age estimates probably should be ± 2 years, as Wolfe suggested. Cementum annulations do not seem to deteriorate under field conditions; I have had little difficulty counting lines in teeth from moose that were estimated to have died more than 20 years ago.

Skeletal remains were sexed on the basis of the presence or absence of antlers or antler pedicels. The stage of antler development also was used to determine the season of death for males. All available bones were checked for abnormalities, and all of the teeth collected. Since 1971, a metatarsus has been collected for use as in index to body size and development.

Fat content of bone marrow is an indicator of the condition of an animal, since the fat stored in marrow of the leg bones is usually the last to be utilized by an animal suffering from malnutrition (Cheatum 1949; Bischoff 1954) (Fig. 28). Because many of the bones from moose killed on Isle Royale were dehydrated when collected, visual descriptions of marrow were used instead of actual fat content (percent dry weight). Visual estimates were compared to actual fat content (expressed as grams of fat/cm^3) for 143 leg bones from 49 moose; such estimates

TABLE 4. Classification of fat content of moose bone marrow.

Visual estimate	Description	Mean fat content (± 95% conf. int.)
Class 1	Solid consistency, lard-like, opaque. Usually cream-colored, pink or yellow.	0.58 ± 0.06 g/cm^3
Class 2	Semisolid consistency, feels somewhat fatty when squeezed between fingers, opaque. Coloration not consistent.	0.43 ± 0.07 g/cm^3
Class 3	Gelatinous consistency, feels watery when squeezed between fingers, translucent. Usually, but not always, red.	0.02 ± 0.01 g/cm^3

Fig. 26. Skeletal remains of moose may remain for decades.

were only accurate enough to assign marrow samples to three broad categories (Table 4). Bone marrow, examined before the present study, was assigned to one of three classes based on marrow descriptions recorded on autopsy cards. Serious fat depletion probably was present in marrow samples from class 3 (lowest fat content), with an occasional specimen from class 2.

Moose Population Structure

Aerial counts were conducted after leaf fall in October 1972–74 to determine the sex and age structure of the moose herd. An additional index of herd composition was obtained using records of moose seen during summer ground work.

During autumn aerial counts a 75-hp Piper J-3 was used. We did not use fixed plots, nor did we attempt complete coverage of the area flown. A high overcast produced the best conditions for observing moose, since sun created shading problems and also seemed to reduce moose activity. Peek (1971a) suggested that fall composition counts could be biased by the tendency of bulls to congregate in the rut and postrut periods, and sometimes by the preference of cows with calves for heavier cover. I attempted to minimize these biases by sampling a wide variety of habitats and by flying overlapping circles.

Moose were sexed by the presence of antlers in males or a white vulva patch in females (cf. Mitchell 1970) (Fig. 29). Moose that did not have visible antlers were inspected on repeated low passes until the presence or absence of a vulva patch was confirmed. Calves were distinguished by relative head and body size (Mech 1966). Bulls with spikes or small forks were considered yearlings. The proportion of yearlings may be somewhat underestimated if there are many yearlings with antlers larger than forks, although this would be offset by 2.5-year-old moose with small antlers.

During ground coverage of the island in the spring-fall period, a record was kept of all moose observed to provide an index of calf abundance. Calves probably are underestimated by this method because cows tend to hide young calves (Pimlott 1959). However, these observations provided both comparative information for fall aerial counts and an index of moose productivity (through occurrence of twins).

Statistical Analysis

Unless otherwise noted, statistical procedures followed Sokal and Rohlf (1969). The significance level for rejection of the null hypothesis was 5%. The P value provided refers to the value obtained in specific cases. A "heterogeneity G-test" was used to detect differences in age distributions of subsamples in the moose-mortality data. In this test, a calculated G value is compared to a critical chi-square value to determine statistical significance. Differences between two percentages were analyzed with the aid of a test statistic (t_s).

a

b

Fig. 27. Annual cementum deposits in moose teeth indicate their age. Cross-section of molar appears in (a), while magnified view of cementum is shown in (b).

Fig. 28. Bone marrow is one of the last fat reserves to be utilized by malnourished moose. This is a fat-depleted example.

Fig. 29. A cow showing white vulva patch characteristic of females, plus mounting marks of bulls during rut.

"ON THE MOVE"

FRED H. MONTAGUE, JR.

2
Ecology of the Wolf

Populations of wolves that are unexploited by man are rare and generally so remote that a long-term study is prohibitively expensive or impractical. National parks provide unique environments in which to observe these important predators. The insular nature of Isle Royale lends special significance to wolf-population studies, for there is relatively little opportunity for transfer between the island and the mainland.

While the wolf population has exhibited great year-to-year stability in total numbers, there have been important variations in its social organization. Since the population is rather small, significant changes in its structure can be linked circumstantially to single events such as the death of an alpha male (Jordan et al. 1967) or possible ingress of a new pack (Wolfe and Allen 1973). The basic, long-term pattern of a single, large pack and several smaller social units has recently changed. In the early 1970s the island supported two large packs that each utilized about half the area. This provided the potential for an increase in total population, and wolf numbers reached a midwinter high of 44 in 1976.

The recent development of a second major pack on the island appears to have resulted from a significant increase in moose vulnerability and a higher beaver population, an important summer prey species. This addition has caused a higher level of predation on moose in winter, especially when deep-snow conditions increased the vulnerability of calves.

Observations of wolves in winter were made either from light aircraft or from the ground using a telescope at long range. Summer observations were limited to a period of several days at one rendezvous site.

Alpha wolves were the only animals consistently identified from year to year. In addition to providing the pack with leadership, they were most active in scent-marking their environment (during winter observations) and were the most active breeders. Alpha wolves restricted the courtship activities of subordinate members of the pack, and mate preferences were demonstrated, both of which contributed to a reduction in courtship behavior and presumably of mating among subordinate wolves.

Numbers and Organization

The recent establishment of a second wolf pack on Isle Royale was a significant departure from the pattern observed in the 1960s, when the population remained remarkably constant. The history of this wolf population has illustrated the effectiveness of natural mechanisms which adjusted wolf numbers to their food base.

A Brief History

Yearly variations in the Isle Royale wolf population are detailed by Mech (1966), Jordan et al. (1967), and Wolfe and Allen (1973). These provide the basis for the following review. During the initial 11 winters of the project (1959–69), the wolf population varied between 17 and 28 (Table 5). The highest population occurred while the large pack was still in operation in 1965; the lowest was in 1969 after 2 years of social instability.

From 1959 through 1966, the population contained only one large pack. For the first 3 years, this pack traveled over the entire island in midwinter; in subsequent years, its movement usually was restricted to the southwestern two-thirds of the island.

The large pack numbered 15–17 wolves from 1959 through 1963. It reached an all-time high in 1964, when 22 wolves were seen. From 1964 to 1966, the pack remained large, at 15–20 wolves. In 1965, a pack of five appeared, believed to have separated from the large pack. This group may have persisted as a pack of four in 1966, although there was some speculation that it left the island in late winter 1965.

In 1966, the large pack initially numbered 15, but three wolves dissociated from the pack shortly after the winter study began. The alpha male, recognizable from 1964 to 1966, developed a limp and was apparently killed by other wolves in March 1966. For the remainder of the 1966 study, the largest group numbered eight wolves. The strong leadership of the alpha male was thought to be instrumental in the maintenance of the large pack, and its fragmentation was linked circumstantially to his demise.

When the 1967 winter study began, two packs (six and seven wolves) were found in the central and southwestern parts of the island. These two packs may have been remnants of the large pack since their travels overlapped considerably. Another pack of four occupied the northeastern end of the island. In February, a pack of seven, including four black wolves, was seen in Amygdaloid Channel, apparently having crossed the frozen channel from Ontario. There was evidence of violence among wolves; a wolf with a bloody head was seen running toward Canada when the "Black Pack" was first seen, and a few days later an injured wolf was observed near the lodge buildings at Rock Harbor. The packs of six and four were not relocated after the Black Pack was seen.

Between 2 and 7 February 1968, two black wolves were observed in a pack of six at the west end of the island. Another pack, numbering seven (the Big Pack) was first seen on 12 February and included one black wolf. While these packs could have been the same, Wolfe and Allen (1973) considered them distinct and suggested that the pack with two black wolves left the island via an existing ice bridge. The single black wolf in the Big Pack was probably one of the four black wolves first seen in 1967. How this wolf became integrated into a resident pack is unknown; Wolfe and Allen (1973) speculated that it could have been associated previously in some way with wolves in this pack, thus implying an additional interchange of wolves between the island and the mainland.

The Big Pack included three wolves that were recognizable from 1968 through 1970—the alpha male and female and the black wolf, a male. The alpha pair was observed mating in 1968. There was mutual courtship observed in this pair in 1969 and 1970, indicating probable mating. In all 3 years, the black male was often seen in the company of the alpha pair and seemed to enjoy special status. Consequently, he was designated the second-ranked, or beta, male. A photograph of the alpha female, taken in 1968 by D. L. Allen, revealed an unusual conformation in her left front leg. By 1972, she had developed a severe limp in this leg and was not seen the following year. The Big Pack persisted into the present study period and became known as the West Pack after the establishment of a second pack in 1972.

Annual Fluctuations, 1971-74

During the present study, the Isle Royale wolf population continued to increase from a low of 17 in 1968 to a high of 31 in 1974. In summer 1971, a second pack became established. During winter studies from 1972 through 1974, each pack occupied approximately half of the island.

TABLE 5. Estimated number of wolves on Isle Royale in midwinter, 1959–76.

Year (Jan.–Mar.)	Known minimum	Best estimate	Source
1959	19	20	Mech 1966
1960	19	22	Mech 1966
1961	20	22	Mech 1966
1962	22	23	Shelton 1966
1963	20	20	Shelton 1966
1964	26[a]	26[a]	Jordan et al. 1967
1965	25	28	Jordan et al. 1967
1966	23[b]	25[b]	Jordan et al. 1967
1967	19[c]	22[c]	Wolfe and Allen 1973
1968	21[d]	22[d]	Wolfe and Allen 1973
1969	14	17	Wolfe and Allen 1973
1970	17	18	Wolfe and Allen 1973
1971	16	20	Present study
1972	22	23	Present study
1973	23	24	Present study
1974	31[e]	31[e]	Present study
1975	41	41	Present study[f]
1976	44	44	Present study[f]
	Average	24.9	

[a]Including one found dead.
[b]Including two found dead.
[c]After presumed ingress of seven wolves.
[d]Before presumed egress of six wolves.
[e]Including one killed in February.
[f]Details of 1975 and 1976 populations will be reported in a later publication.

1971. The Big Pack (hereafter referred to as the West Pack) was recognized in 1971 by the presence of the black male and alpha female. The black male was clearly the alpha male, replacing the large gray male that had been dominant from 1968 through 1970. Although ten members were seen twice, the pack usually numbered seven to nine wolves. On the basis of limited behavioral information, two pups were believed present in the pack. The pack ranged over the southwestern third of the island, venturing northeast as far as the middle of Siskiwit Lake.

In addition to the main pack, three duos were observed: one traveled among the peninsulas of the northeast end of the island, a second duo ranged from Moskey Basin through Chippewa Harbor to Wood Lake, and a third inhabited the shoreline of Siskiwit Bay, traveling between Houghton Point and Malone Bay.

Four single wolves also were recognized, with their respective activities centered at the southwest end, northeast end, the north shore west of Todd Harbor, and Malone Bay.

While the maximum number of wolves seen on a single day was 16, the presence of three duos and four singles was well established, and the population may be summarized as follows:

West Pack	10
Duos (3)	6
Singles	4
	20

1972. Two packs (West and East) accounted for most of the island's wolves from January to March 1972. Each pack commonly numbered eight wolves in late January, but consistently numbered seven and ten, respectively, after mid-February. The ranges of these packs did not overlap—each occupied about half of the island. In addition, a trio of wolves operated in the Malone Bay-Siskiwit Bay area, with tracks suggesting that they ranged along the shore of the island as far as Chippewa Harbor.

The East Pack had its origins within the wolf population present the previous winter, since there was no ice bridge to Canada in the interval between the winter studies of 1971 and 1972. Besides the alpha male and female there were six wolves that were uniform in size and body markings, virtually indistinguishable during observations or in photographs (Fig. 30). All six had the physical appearance of pups—presumably a litter from the alpha pair. This conclusion was supported by the fact that the alpha male was never observed chasing any of these six wolves away from the alpha female during the mating season.

In 1972 the alpha wolves in the West Pack were the same individuals as in 1971—the black male and small, gray female (Fig. 31). Although no other wolves in the pack were identifiable from 1971, the presence of pups was not confirmed. In spite of a limp, the alpha female was able to retain her dominant status, though occasionally she had trouble keeping up with the other wolves in the pack. I saw this female for the last time in May 1972, when she walked, still limping, along the

shore of an inland lake with the black male; her summer coat was quite reddish. In September 1972, the black male, a smaller, reddish wolf (probably the alpha female), and three gray wolves were seen lying on an open ridge (Coley Thede, pers. comm.). The black alpha male and female apparently died between September 1972 and January 1973. The black male was then at least 6.5 years old, since he was first observed in 1967. The alpha female was also at least 6.5 years old when she died, because she mated in 1968 and had to be at least 22 months old at that time. She was probably older, since it is rather unlikely that she could have reached the position of alpha female by her second year.

On 24 February, a total of 20 wolves was observed (packs of seven and ten plus the trio). It was obvious from tracks on fresh snow that at least two single wolves were also present—one in the vicinity of Chippewa Harbor and one on the north shore near Little Todd Harbor. On 3 March, a wolf was seen following and apparently trying to remain hidden from the pack. Accordingly, the population totaled:

West Pack	7 + 1
East Pack	10
Malone Bay trio	3
Singles	2
	23

1973. The East and West packs, numbering 8 and 13 wolves, were again well defined. Spatial arrangements between the packs were similar, although their travels overlapped along the north shore of the island, where they visited each other's kills. On 24 and 25 February, a total of 23 wolves was seen. The final population estimate was:

West Pack	8
East Pack	13
Todd duo	2
Single	1
	24

The "Todd duo" was seen only three times. Judging from tracks, most of their activity was centered in the Todd Harbor area, although once they traveled from Little Todd Harbor to Lake Whittlesey. The loner, positively identified as a male, was seen only once, but tracks indicated that he ranged along the north shore from a point opposite Lake Desor to the northeast end of Amygdaloid Island, a distance of 40 km.

The leadership of the West Pack had changed completely since the previous year—a new alpha pair had replaced the black male and his limping mate. From

their appearance and, especially, their behavior, four wolves in this pack were classed as pups. One of these disappeared from the pack around 20 February and was not seen again.

The East Pack numbered 12 or 13 for the entire winter study. Observations were hampered by the wolves' extreme avoidance of the study plane, probably resulting from disturbance by other aircraft earlier in the winter. The alpha pair had not changed from the previous year (Fig. 32). The number of pups was estimated from the increase in maximum pack size from 1972 to 1973—certainly a minimum figure since it assumes no mortality in the intervening year.

1974. Both main packs increased in size from 1973, and a duo and at least one single were present. The 31 wolves observed on 17 February provided the following minimum count:

West Pack	12
East Pack	16
Todd duo	2
Single	1
	31

Again, each pack inhabited its respective end of the island, but movements of the East Pack into West Pack territory increased the amount of overlap. Two wolves again were active in the Todd Harbor area, quite possibly the duo of 1973.

In late January, the West Pack numbered 11 or 12. The increase in pack size from 1973 indicated the presence of at least four pups. Early in February, the pack broke into several smaller groups, and the alpha male, recognizable from 1973, was the dominant wolf in one group of four. His mate, the alpha female, was also in this group—there was some uncertainty that this was the same female as during the previous year. A single wolf was tolerated by this group near a kill, and it was probably one of the original pack members. Several days later, another group of four was seen leaving a kill in the interior of the island. Two other wolves, soon joined by a single, were observed in the Washington Harbor area, and this trio stayed together for the remainder of the study period. Since no other wolves were seen in the West Pack's range, it appeared that the West Pack had broken into units of 4, 3, 3, and 1. The 4 wolves, one group of 3, and a single wolf reunited in March, forming a pack of 8.

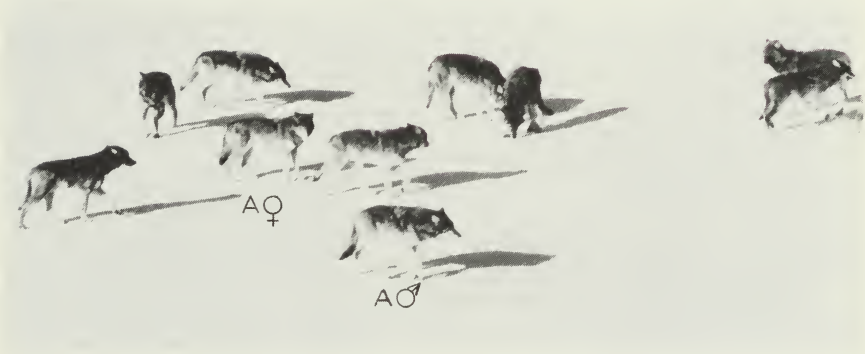
Winter Movements

On Isle Royale, wolf movements in winter vary from year to year, depending on snow conditions and the presence of shoreline ice. Extensive travel within a pack's range is necessary to locate vulnerable prey; such travel is lowest in years when vulnerable prey are abundant.

Fig. 30. Alpha pair (female facing right) and six probable pups in East Pack, 1972.

Fig. 31. West Pack alpha pair (male is black), 1972. Note crooked front leg of alpha female.

a



b

c

Fig. 32. East Pack alpha pair in 1972 (a), 1973 (b), and 1974 (c). Alpha female was the same wolf all 3 years; alpha male the same in 1972 and 1973.

Travel Routes

Natural topography determines the ease of travel in different areas of the island, with the principal avenues for wolf movements consisting of chains of lakes, shorelines, old beachlines of Lake Superior, and bedrock ridges. The shorelines of the island stand out as principal hunting areas for wolves. Moose often seek conifer cover in winter, and since most of the conifer cover on the island is located in predominantly spruce-fir forests near lake level (Linn 1957), moose densities in midwinter tend to be highest along lakeshores. This creates an optimum hunting arrangement for wolves. Of a total of 325 wolf-killed moose located in winters from 1959 through 1974, 45% were within 200 m of either Lake Superior or Siskiwit Lake, a large interior lake.

The distribution of wolf-killed moose from 16 winter periods further suggests that some areas of the island produce more favorable hunting conditions than others. Kill density is obviously high in the area of North Gap (mouth of Washington Harbor), Malone Bay, Chippewa Harbor-Lake Mason, and Blake Point. All of these locations receive a high level of hunting effort in winter either because they are land masses lying between frozen lakes or bays, or because many travel routes intersect in those areas. Blake Point was hunted by a large pack in 1972 for the first time in several years, and perhaps a high proportion of vulnerable moose had been allowed to accumulate there. Other areas, notably the 1936 burn, have produced few kills in recent years, probably because of a gradual reduction in use of old burns by moose and unusually deep snow in several recent winters that restricted moose to more dense forest types.

Travel routes of the East and West packs during winters 1972-74 are shown in Figs. 33-35, along with locations of old and fresh kills. With the exception of the West Pack in 1974 (which fragmented and was impossible to track adequately), the routes shown represent continuous movements during the period of study. Variations in extent of travel and actual routes used are explained below in relation to snow and ice conditions.

EFFECT OF SHORELINE ICE

Travel around the perimeter of the island was extensive in 1972 and 1974, but quite reduced in 1973 (Figs. 33–35). In both 1972 and 1974, shelf ice was continuous around the island for most of the study period, and shorelines were used commonly by wolves (Fig. 36). In contrast, little shelf ice formed in 1973, and wolves had to travel onshore. Similarly when there was no shelf ice in 1969, wolves made extensive use of the interior even though snow was exceptionally deep (Wolfe and Allen 1973).

Occasionally, wolves venture onto ice that is very thin, especially if it is covered with snow. One morning in February 1974, the East Pack rested within 50 m of the edge of the shelf ice near Houghton Point. Tracks of one wolf led directly to the edge and then back to a resting place close to the other wolves. In the afternoon, the thin ice where the wolf had walked broke off and floated away.

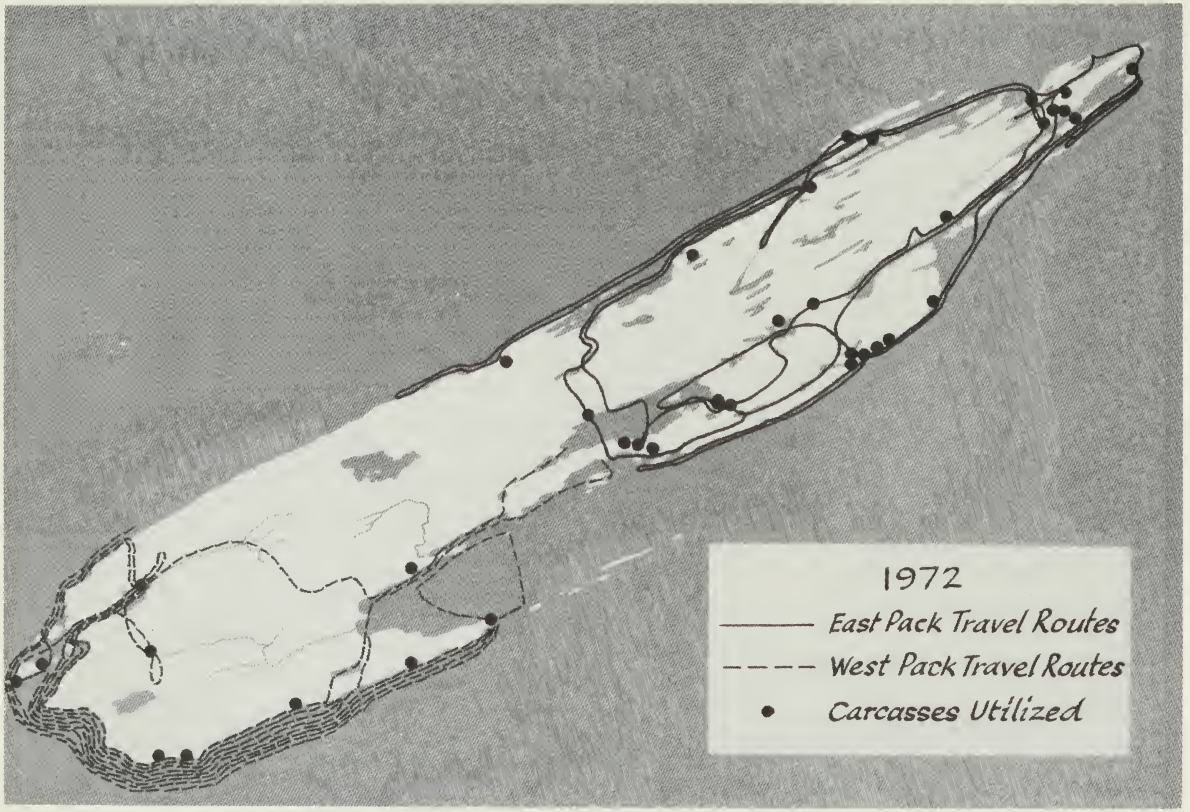


Fig. 33. Travels and kills of the East and West packs, January-March 1972.

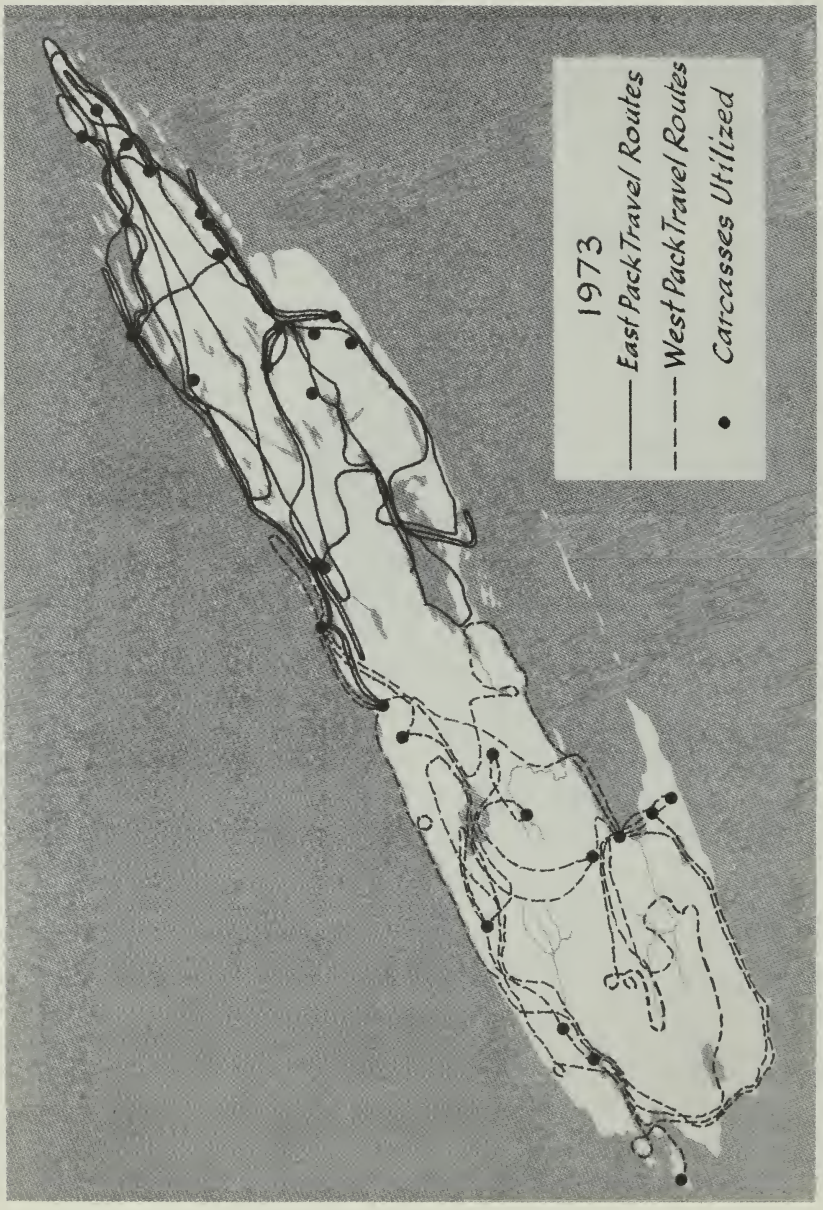


Fig. 34. Travels and kills of the East and West packs, January-March 1973.

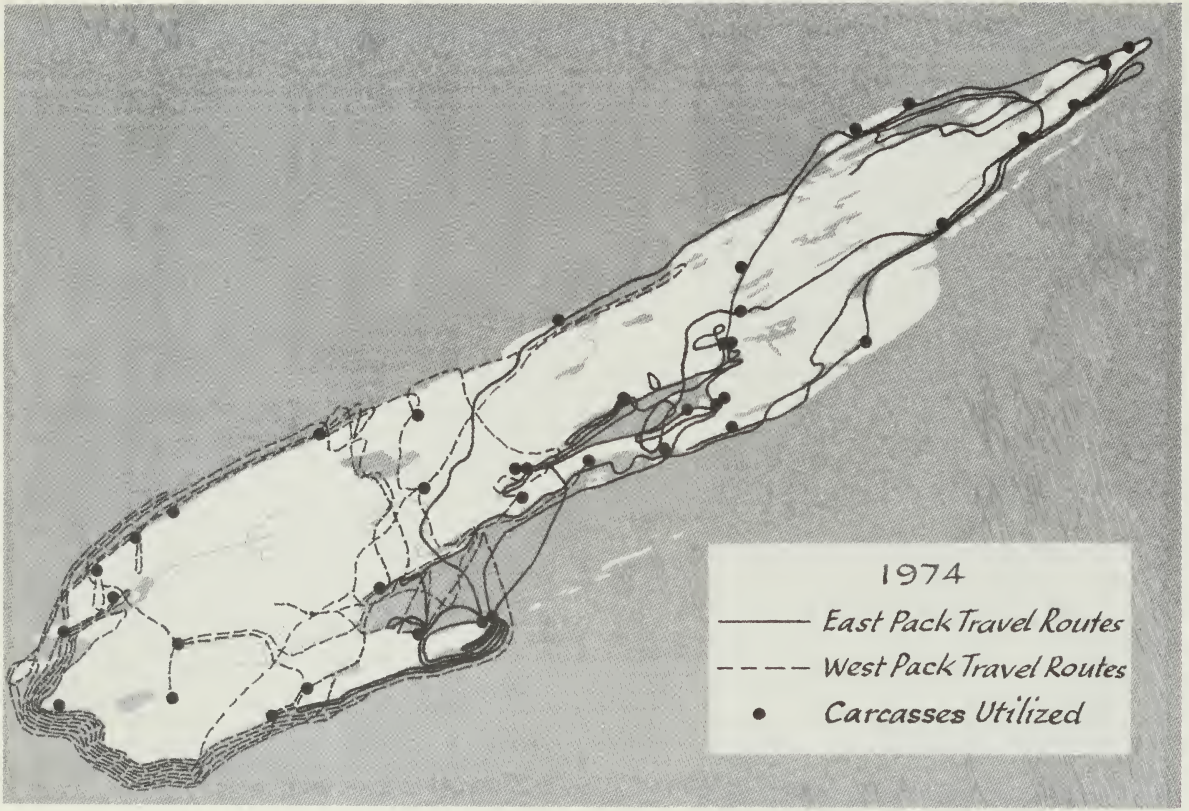


Fig. 35. Travels and kills of the East and West packs, January-March 1974.

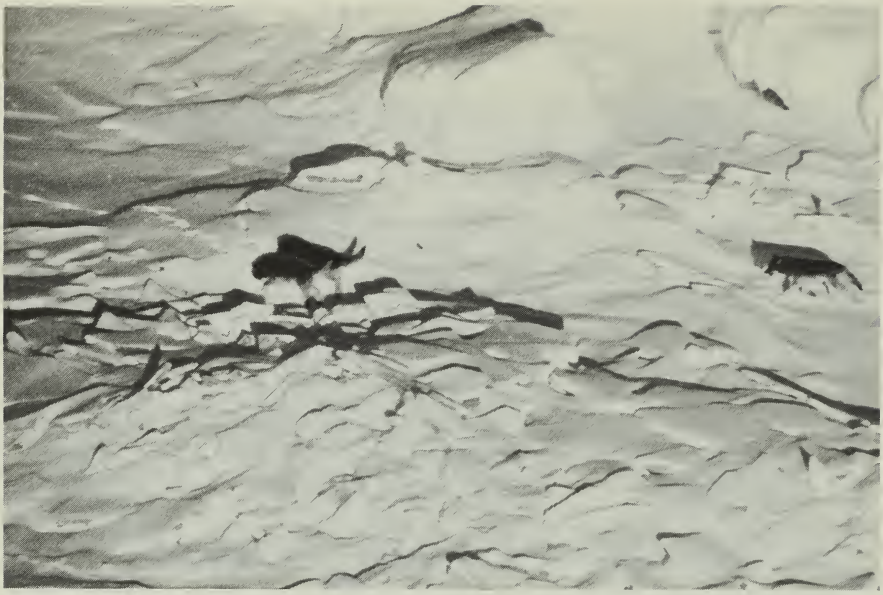


Fig. 36. Wolves frequently use shelf ice while traveling.

EFFECT OF SNOW CONDITIONS

Relative to moose, wolves have a lighter foot loading (weight-load-on-track) and consequently receive greater support from snow of a given density. Weight-load-on-track for five wolves in the Soviet Union ranged from 89 to 114 g/cm^2 (Nasimovich, 1955). In contrast, a cow and calf necropsied on Isle Royale in 1973 had foot-loadings of 488 g/cm^2 and 381 g/cm^2, respectively. Measurements by others range from 420 g/cm^2 to over 1000 g/cm^2, depending on the sex and age of the moose (Nasimovich 1955; Kelsall 1969; Kelsall and Telfer 1971).

Moose rarely receive consistent support from crusts on the surface or within the snow profile (Kelsall and Prescott 1971), and wolves often have a considerable advantage when crusts are strong enough to support them. For example, in 1972, wolves on Isle Royale appeared to be supported by a crust located 20 cm below the surface of the snow, although moose calves broke through and moved with difficulty. Crusting conditions and frequent thaws (which increase snow density) during the entire 1973 winter study allowed wolves to travel with relative ease throughout the interior of the island (Fig. 34). Similar conditions prevailed during the first half of March 1974. At such times moose usually remained in areas of conifer cover, and their movements seemed greatly restricted.

Since wolves have relatively short legs, they are greatly handicapped by deep, soft snow. Nasimovich (1955) found that wolves sank to their chests in snow of density 0.21 or less, which describes essentially all fresh-snow conditions. Thus,

wolves generally travel in single file through snow, and have been observed moving into this formation in response to as little as 20-25 cm of snow along lake edges (Fig. 37). Nasimovich also found that wolves had difficulty chasing ungulate prey when snow depths exceeded 41 cm, and, with depths greater than 50–60 cm pursuit through untracked snow was almost impossible. In 1971, 41 cm of fresh snowfall on a 51-cm base precluded extensive travel by wolves in the interior of the island. Frequent fresh snow in 1972 kept depths in open areas above 75 cm, and, in spite of a crust within the snow profile, movements of wolves usually were limited to shorelines. The distribution of wolf-killed moose illustrates one effect of deep snow. When snow depth exceeded 75 cm, there was a significant increase in the number of kills located within 0.8 km of a shoreline, although part of this increase is related to changes in moose distribution.

Distance Traveled by Wolf Packs

Since most pack movements involve hunting, the amount of travel should roughly reflect success and, indirectly, the relative abundance of vulnerable prey. Average distances traveled by Isle Royale packs between kills are quite variable in different years (Table 6), ranging from a low of 18.5 km/kill to a high of 54.1/kill.

Highest travel per kill was shown by both East and West packs in 1973, a year when the average daily mileage was also highest for both groups. This suggests that moose vulnerability was lowest in 1973, a hypothesis supported by the fact that calves were killed least often in that year. Frequent snow crusts which made travel for wolves relatively easy contributed to the greater movements in 1973.

Minimum movement between kill (18.5 km) was registered by the West Pack in 1971, when wolves had little trouble finding vulnerable prey, especially calves, along shorelines. Even shorter distances were reported by Kolenosky (1972), who found that a pack traveled only 14.7 km between kills of deer in Ontario during 1969 when deep snow rendered deer more vulnerable and probably reduced wolf movements.

Food Economy of Isle Royale Wolves

Fundamentally, predator-prey interaction involves energy transfer from one trophic level to another, as from herbivore to carnivore. The complexity of this energy transfer is directly related to the number of species in a particular food web. On Isle Royale, the wolf, the major carnivore, is entirely dependent on moose and beaver, which are primary consumers of vegetation. This is a relatively simple system compared to the food web described by Cowan (1947) for the Rocky Mountain national parks of Canada, where wolves depended heavily on elk but also killed deer, moose, bighorn sheep, caribou, and, at certain seasons, snowshoe hare and beaver.

Fig. 37. Wolves usually travel single-file through snow.

TABLE 6. Travel estimates for wolf packs, 1971–74.

Year	Period of coverage	Travel per day (km)	Average movement between kills (km)
	West Pack		
1971	2 Feb.–9 Mar. (35 days)	9.0	18.5
1972	27 Jan.–9 Mar. (42 days)	9.5	39.8
1973	25 Jan.–26 Feb. (32 days)	15.1	54.1
	East Pack		
1972	27 Jan.–9 Mar. (42 days)	10.5	25.6
1973	25 Jan.–4 Mar. (38 days)	13.5	42.8
1974	24 Jan.–10 Mar. (45 days)	9.8	32.8

Total days tracked = 234.
Total distance tracked = 2608 km.
Average travel per day = 11.1 km.
Average travel per kill = 33.0 km.

Isle Royale wolves prey on moose at all times of the year, while beaver are available only during the ice-free season. While quite variable from 1971 to 1974, the entire food base of the Isle Royale wolves was probably higher in the early 1970s than during the previous decade, owing to increased vulnerability of moose (at least in winter) and an increased beaver population. This is probably why the island was partitioned into two pack territories after 1971.

The Wolf as a Predator of Big Game

Food habits of wolves have been studied intensively, mainly because of human concern for the prey species, domestic or otherwise. Wolves are well adapted both physically and behaviorally for predation on large mammals, and an absence of large ungulate prey may adversely affect resident wolf populations, especially pups (see Pup Production).

Food habits of wolves seem to be most variable in tundra areas where wolves typically prey on a single ungulate species. Clark (1971) found wolves in central Baffin Island to be almost completely dependent on caribou, while Tener (1954) indicated snowshoe hares as the principal prey species for wolves on Ellsmere Island. Wolves denning in the northern Brooks Range in Alaska often ate small rodents, birds, fish, and insects, although Stephenson and Johnson (1972) believed that wolves nonetheless depended primarily on ungulates. Pimlott et al. (1969) pointed out that wolves have never been shown to thrive for a significant period on prey smaller than beaver, and most biologists agree that wolves are characteristically dependent on large mammals.

Moose, white-tailed deer, and beaver are the principal prey species of wolves in mainland areas adjacent to Lake Superior (Thompson 1952; Stenlund 1955; Pimlott et al. 1969; Mech and Frenzel 1971). Prey size and numbers determine which species are most important for the wolf. Where deer are available they are highly preferred (Pimlott et al. 1969; Mech and Frenzel 1971). Since beaver are small and, presumably, easily killed by wolves, predation on them is determined largely by availability.

Nonwinter Food Resources

Analysis of wolf scats collected in 1973 showed that Isle Royale wolves preyed on beaver to a much greater extent than a decade earlier (Fig. 38). A sample of 554 wolf scats was collected in 1973 from homesites and game trails used by both packs (Table 7). Most of these were from 1973, although a small proportion of the scats collected at the East Pack den were probably from 1972.

Beaver and moose calves together constituted 90.0% of the food items in nonwinter scats. Remains of beaver (hair and occasionally claws) were found in 75.8% of the total scat sample and made up 50.5% of 831 prey occurrences. Moose hair occurred in 69.3% of the scats and comprised 49.5% of the total food items.

TABLE 7. Occurrence of prey remains in wolf scats, 1973.

Source	Total scats	Vertebrates Identified: Moose adult	Moose calf	Unident. moose	Beaver	Hare	Bird	Total
Spring and Summer Scats Before Calf Molt (Early August)								
East Pack den	124	13	68	8	90	–	–	179
East Pack rend. No. 1	40	3	29	1	34	–	–	67
East Pack rend. No. 2	128	11	65	8	109	–	–	193
Total	292	27	162	17	233	–	–	439
% frequency of occurrence		6.2	36.9	3.9	53.1	–	–	100.1
% frequency in scats		9.2	55.5	5.8	79.8	–	–	
Summer and Fall Scats After Calf Molt (Early August)[a]								
East Pack rend. No. 3	78	17	37	10	59	–	–	123
East Pack rend. No. 4	74	41	17	7	59	1	1	126
West Pack rend.	110	42	22	10	69	–	–	143
Total	262	100	76	27	187	1	1	392
% frequency of occurrence		25.5	19.4	6.9	47.7	0.3	0.3	100.1
% frequency in scats		38.2	29.0	10.3	71.4	0.4	0.4	
Composite total	554		409 (all moose remains)		420	1	1	831
% frequency of occurrence			49.2		50.5	0.1	0.1	99.9
% frequency in scats			73.8		75.8	0.2	0.2	

[a]The calf molt probably results in hair from calves actually identified as "adult," and thus scats deposited after this time do not accurately reflect calf/adult proportions.

Of the identifiable moose remains (in scats deposited before the change in calf pelage in early August), 85.7% were from calves. Hare and bird remains were identified from only one scat and are unimportant as prey. While the 1973 blueberry crop was the best remembered by many long-time island residents, fruit was not found in any of the scats. Vegetation (mostly grass) was found in 6.1%, and unidentified seeds in 2.2% of the scats. These nonanimal items were not tallied in Table 7. Murie (1944) suggested that grass may act as a scouring agent against intestinal parasites, a hypothesis supported by his discovery of roundworms among blades of grass in some scats. An 18-inch section of tapeworm (*Taenia* sp.) was found in a fresh Isle Royale wolf scat containing grass, and Kuyt (1972) reported a similar finding.

INCREASED PREDATION ON BEAVER

The incidence of beaver remains in fresh scats from 1958 to 1960 was 13.1% (Mech 1966) (Fig. 39). In the following 3-year period beaver occurrence was essentially the same, 15.6% (Shelton 1966). Although there were no systematic scat collections in subsequent years, field examination of scats found incidental to other work showed no obvious changes (Jordan et al. 1967; Wolfe and Allen 1973). However, the 1973 data clearly demonstrate a significant increase in predation on beaver (t_s = 13.7, P 0.001) since 1958-63 (Table 8).

In the decade between the scat analyses, the beaver population doubled, with the estimated number of active colonies (determined from aerial count) increasing from 140 in 1962 to 300 in 1973 (Shelton, unpubl. data). During the same period, wolf predation on beaver tripled, wtih percentage of beaver in wolf scats increasing from 14.4% to 50.5%.

Pimlott et al. (1969) found that the frequency of beaver in wolf scats in the Pakesley area of southern Ontario was 59.3%, compared to 7.1% in nearby Algonquin Park. A study by Hall (1971) showed that the beaver population in the Pakesley area was at least three times more dense than that of Algonquin Park. Clark (1971) pointed out that increased predation on beaver at higher densities could result from a shift in hunting effort to the more abundant beavers or simply from an increased frequency of encounters between wolf and beaver. Hall (1971) reported an increase in predation on beaver and a decrease in predation on deer in Pakesley during the 1960s, corresponding to changes in densities of these two prey species. He believed this indicated a shift in hunting effort.

On Isle Royale, known wolf trails often parallel water courses and pond edges, but we do not know whether predation on beaver is limited to chance encounters or whether purposeful hunting is important. Field observation did not indicate depression of beaver numbers around wolf homesites. Some of these were adjacent to active beaver ponds, suggesting that wolves did not spend a lot of time stalking and hunting beaver.

Fig. 38. Scat analysis was used to determine summer wolf diet.

Fig. 39. Beavers are an important prey for wolves in summer.

TABLE 8. Beaver occurrence in summer wolf scats, and beaver population trends.

Period	Total number of summer scats (no. occurrences)	% frequency of occurrence of beaver in wolf scats[a]	Estimated number of active beaver colonies[b]
1958–60	205 (214)	13.1[c]	–
1961–63	232 (237)	15.6[d]	140
1973	554 (831)	50.5	300

[a]Only moose and beaver occurrence considered.
[b]Beaver population estimated by Shelton (1966; unpubl. data).
[c]Mech (1966).
[d]Shelton (1966).

The relative levels of predation on moose and beaver as indicated by scats were consistent throughout spring-fall 1973 (Table 9). Shelton (1966) found a slight increase in beaver occurrence in wolf scats in the fall, when beaver are actively cutting winter stores of food and consequently are more vulnerable. Although scats from the last East Pack rendezvous did not indicate any increase, most of the scats from this area probably dated from August and early September, before intensive cutting begins.

While it is difficult to estimate the current importance of beaver to Isle Royale wolves in terms of biomass or numbers of prey, a comparison with other studies provides a rough assessment. The highest reported occurrence of beaver in wolf scats came from studies in the Pakesley area of Ontario. Beaver remains were found in 62% of the scats examined in 1960, and beaver comprised 59% of the total food items (Pimlott et al. 1969). By 1964, the frequency of occurrence of beaver in wolf scats in Pakesley had increased to 77%, and beaver were regarded as the primary summer prey of wolves (Hall 1971; Kolenosky and Johnston 1967). The incidence of beaver in scats from Isle Royale wolves (76%) and the percentage of beaver in total food remains (51%) are second only to the reported data for the Pakesley area.

A high beaver population on the northeastern half of the island may have been an important factor allowing rapid growth of the East Pack (from 8 to 10 in 1972, to 16 in 1974). Over a 3-year period a minimum of 13 pups survived to midwinter in this pack. The general appearance in July of the 1973 pups and the rapid growth of at least two of them between observations in July and August suggest an abundant food supply. The dense beaver population probably has been an important factor ensuring high pup survival at a time when the production of moose calves, the other principal summer prey, was subnormal.

TABLE 9. Incidence of beaver and moose remains in wolf scats from various homesites and associated trails, 1973.[a]

	East Pack					West Pack	
Site	Den	Rend. No. 1	Rend. No. 2	Rend. No. 3	Rend. No. 4	Rend.	Total
Approximate date of occupancy	Late April–late June	Late June–21 July	19 July–29 July	27–28 July–23–24 Aug.	20 Aug.–early Oct.	Late July, early Aug.	
Total scats (no. occurrences)	124 (179)	40 (67)	128 (193)	78 (123)	74 (126)	110 (143)	554 (831)
% beaver	50.3	50.7	56.5	48.0	46.8	48.3	50.5
% moose	49.7	49.3	43.5	52.0	53.2	51.7	49.5

[a]Only moose and beaver considered, since other occurrences were insignificant.

Winter Predation Patterns

Winter food habits determined from direct observations and aerial tracking showed that wolves on Isle Royale continue to subsist in winter almost entirely on moose. The snowshoe hare population was relatively low during this study, and while wolves occasionally flushed hares during observations, they never gave chase. No indications of wolf predation on hares in winter were found. Beaver were available only in rare instances when they ventured from beneath the ice to cut food. During mild weather between January and March 1973, we discovered two wolf-killed beaver. Likewise, during a thaw in March 1974, one or more beaver were killed on the Big Siskiwit River.

Although wolves rarely find active beaver in winter, they show great interest in beaver lodges and dams encountered during their travels (Fig. 40). The East Pack even dismantled a lodge in February 1973, near Harvey Lake. The wolves had killed two moose within 100 m of the lodge, and their activities while in the area for several days centered on digging out the lodge.

HUNTING SUCCESS

In forested regions such as Isle Royale, wolves depend heavily on their sense of smell for prey detection. Of 30 observations of wolves detecting moose from 1972 to 1974, it was possible to determine the method of prey detection 17 times. In 10 cases in which wolves caught the scent of a moose, they either approached directly upwind or turned toward their prey after crossing downwind from the moose. Mech (1966) reported that wolves seemed to sense prey 2.4 km away, underscoring their olfactory sensitivity. Wolves visually detected moose six times, and once they followed a fresh moose track to the animal.

Mech (1966, 1970) provided an extensive discussion of the results of moose-wolf encounters observed in the first three winters of the project. The basic pattern he observed has not changed significantly. Moose that stand their ground when wolves approach are not killed; all observed encounters on Isle Royale that ended in a kill occurred after the victim initially ran from wolves. For unknown reasons, vulnerable moose do not stand and face wolves when first approached. While chasing a moose, wolves apparently respond to vulnerability cues that are not obvious to aerial observers; sometimes they quit immediately, at other times the chase might last for long distances (Fig. 41).

The primary point of attack is the hindquarter region of the moose, where wolves can dash in and out and stand the best chance of avoiding the quick strikes of the hooves. When wolves inflict serious wounds, they are often content to wait until the moose weakens. In February 1972, however, the East Pack, after spending most of a night close to a wounded adult near Lake Richie, abandoned the animal around daybreak. The moose continued to stand in heavy cover that morning, but by afternoon was lying on its side. This was an 8-year-old cow in apparently good condition, with abundant marrow and visceral fat reserves and

Fig. 40. Wolves investigating beaver lodge.

pregnant with one fetus. She had deep wounds around the anal opening and had apparently lost a considerable amount of blood. In the next 5 weeks, the East Pack never returned to the carcass, but by early May the wolves had consumed it entirely.

Mech (1966) found that wolves have a low rate of hunting success, presumably because most of the moose they encounter are not vulnerable. Of 77 moose tested by wolves, 6 were killed. From 1972 to 1974, 38 moose were tested during observations, and only one was killed. A schematic representation of results of moose-wolf encounters in the two periods is presented in Fig. 42. Observations of hunts in the recent period were too few to determine changes in hunting success.

EFFECT OF SNOW CONDITIONS

Crusts within the snow profile or on its surface provide support for wolves but interfere with moose movements. Since crusts are frequent on Isle Royale, deep snow often results in increased hunting success for wolves. This was apparent in 1969 when more kills were found than in any previous winter (Appendix L). An increased kill rate on Isle Royale was also evident in the "deep snow" winters of 1971 and 1972. In all three of these winters, the degree of carcass utilization was noticeably less, indicating higher hunting success (Wolfe and Allen 1973; Peterson and Allen 1974) (Fig. 43).

Increased calf vulnerability due to reduced mobility in deep snow is reflected in a high kill of moose calves when snow depths exceed 75 cm (Fig. 44). Most calves are killed near shorelines, which are traveled heavily by wolves when snow is deep

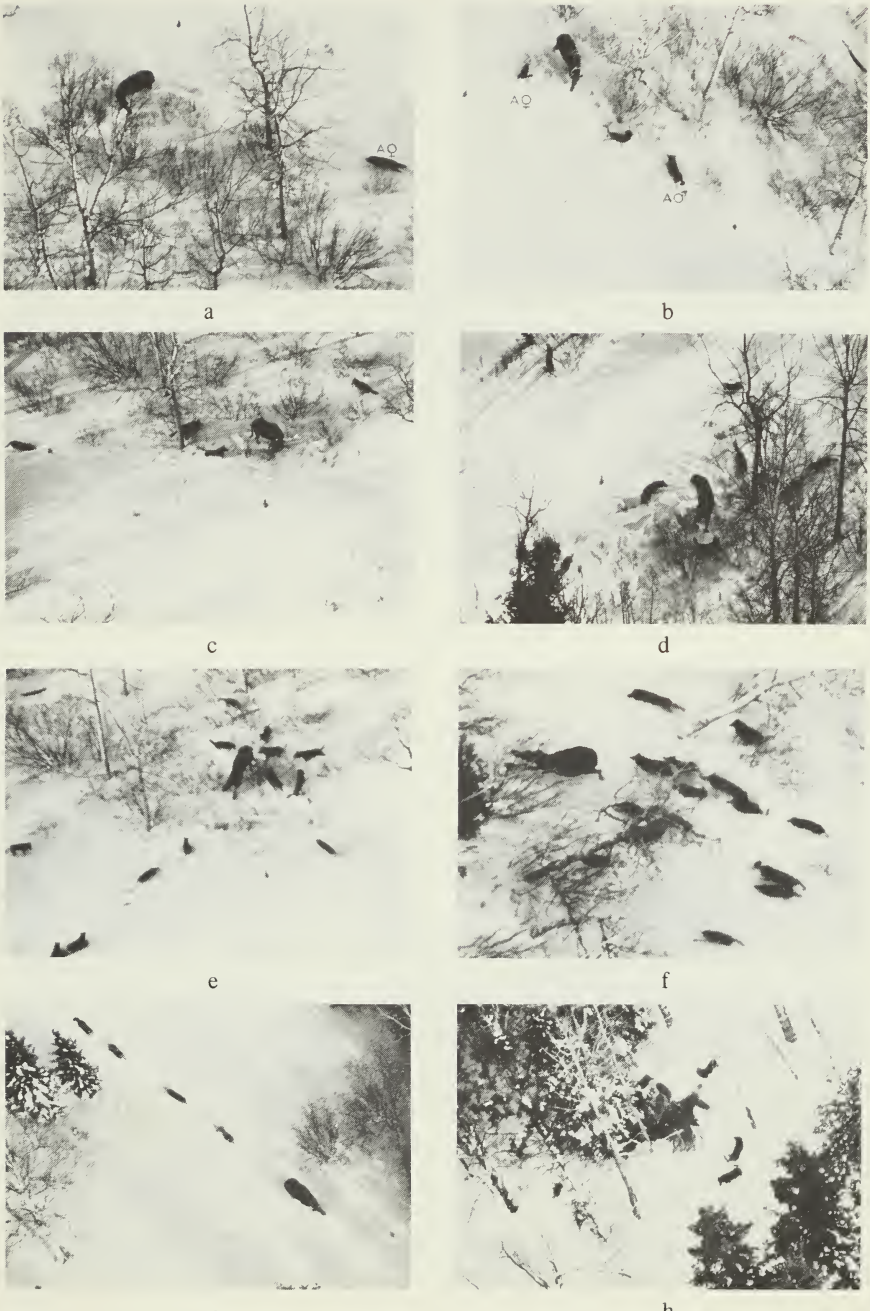


Fig. 41. East pack in successful chase. Victim was 16-year-old cow with arthritic hip and vertebrae and was pulled down within 2 minutes. Alpha wolves indicated.

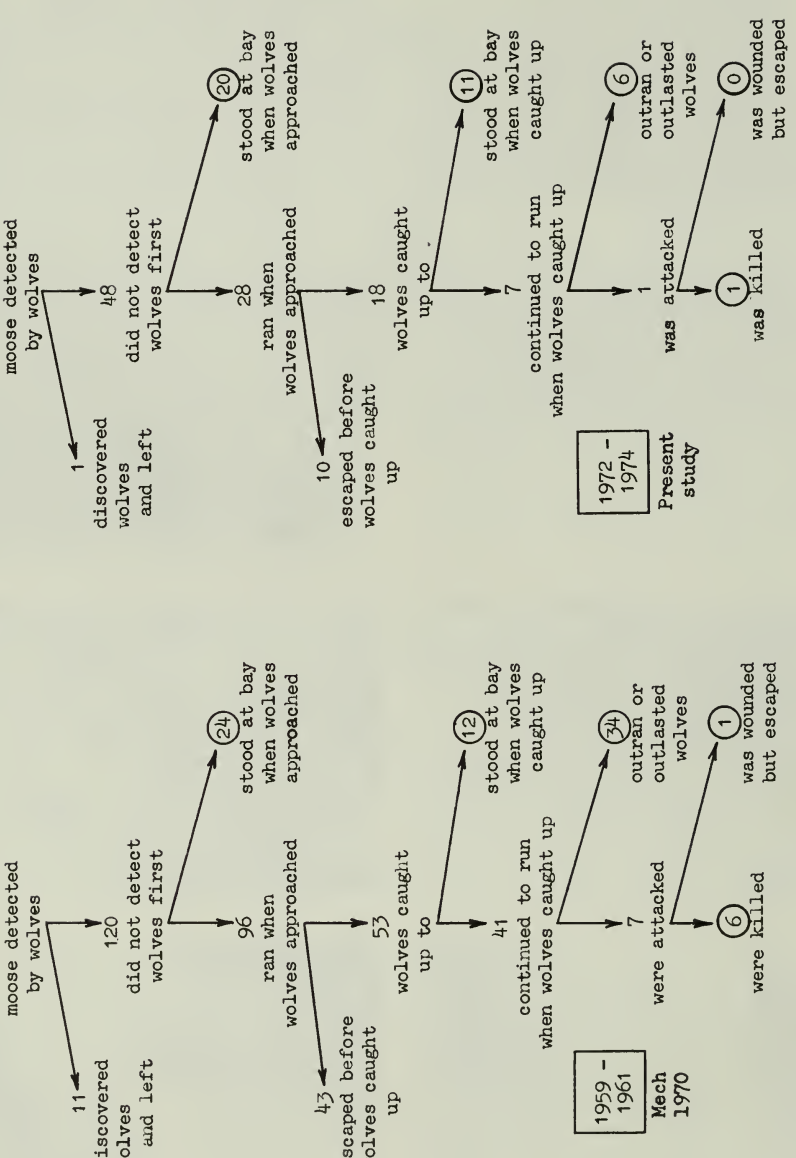


Fig. 42. Results of observed moose-wolf encounters on Isle Royale, 1959-61 (Mech 1970:210) and 1972-74 (this study).

Fig. 43. Carcasses of wolf kills were often underutilized in the early 1970s.

Fig. 44. East Pack (1973) in unsuccessful chase. Note cow at rear of calf.

and shelf ice present. Calves may be so restricted that they are left in shoreline areas by their mothers who have gone elsewhere to feed. In 1972, the West Pack encountered two adults and a calf on the south shore. Both adults ran along the shore, but the calf headed inland and was pulled down by wolves within 100 m. Either the calf's mother was behaving in a highly abnormal fashion or she was not present. In 1971, we saw two calves without a mother present; one of these was killed by a single wolf (Peterson and Allen 1974).

WINTER FOOD AVAILABILITY

Estimates of food consumption by wild wolves usually are derived by multiplying the average weight of prey by the number killed in a specific period (Mech 1970). When calculated in this manner, food *availability* rather than actual consumption is estimated, since utilization of carcasses varies considerably with the size of the pack, size of prey killed, and the ease with which additional prey may be taken (Fig. 45). In winters when moose are more vulnerable to wolves, the kill rate may go up, while the corresponding degree of carcass utilization declines. The calculated availability of food for Isle Royale wolves is most useful for comparisons of hunting success.

Whole weights of several Isle Royale moose (Appendix E) provided the basis for estimates of the potential food contributed by each bull, cow, and calf (assumed average whole weights of 432, 364, and 159 kg, respectively). The primary inedible portions of a moose are the stomach contents and some of the hide and skeleton. The stomach of a 400-kg bull necropsied in February weighed 65 kg, or about 16% of its body weight. Inedible stomach and intestinal contents of adults were assumed to weight 68 kg, and an additional 34 kg were subtracted for portions of hide and skeleton usually left uneaten. Stomach and intestinal contents of calves were assumed to weigh half those of an adult, or 34 kg. Although wolves sometimes eat the entire skeleton and hide of calves in winter, 11 kg were subtracted for parts usually left uneaten. Thus the potential food of each bull, cow, and calf when killed by wolves is a calculated 330, 261, and 114 kg. Adults of unknown sex were assumed to contribute 295 kg. Carcasses of moose collected for necropsy were consumed by the West Pack; weights of these carcasses were included in the calculations for the West Pack on the assumption that the wolves would have otherwise killed a moose themselves (Fig. 46).

From 1971 through 1973, calculated availability of food for both East and West packs varied between 6.2 and 10.0 kg/wolf/day, while in 1974 daily figures for both East and West packs dropped to 5.0 and 4.4 kg/wolf, respectively (Table 10). The drop in availability of food in 1974 stems largely from the increase in pack sizes from 1973 to 1974 and the fact that a high percentage of the kills were calves. Winter availability of food on an individual basis declined for each pack through the period of study, partially reflecting a decline in ease of prey capture from winters in 1971 and 1972 when unusually deep snow contributed to a high kill-rate.

Fig. 45. Wolves feeding on carcass.

Fig. 46. Wolves bedded near kill.

TABLE 10. Estimates of food availability for West and East packs, 1971–74.

West Pack					East Pack				
Year	Dates	No. wolves	Moose killed	Prey available per wolf per day (kg)	Year	Dates	No. wolves	Moose killed	Prey available per wolf per day (kg)
1971	2 Feb.– 9 Mar. (35 days)	(8)–10	3 bulls 5 cows 11 calves	10.0[a]					
1972	27 Jan.– 9 Mar. (42 days)	8	3 bulls 2 cows 6 calves	7.4[b]	1972	27 Jan.– 9 Mar. (42 days)	10	6 bulls 3 cows 1 unk. ad. 7 calves	9.2
1973	25 Jan.– 26 Feb. (32 days)	8	3 bulls 2 cows 1 unk. ad. 3 calves	8.5[c]	1973	25 Jan.– 4 Mar. (38 days)	13	3 bulls 6 cows 1 unk. ad. 2 calves	6.2
1974	21 Jan.– 12 Mar. (50 days)	12	2 bulls 2 cows 1 unk. ad. 10 calves	4.4	1974	24 Jan.– 10 Mar. (45 days)	16	4 bulls 5 cows 2 unk. ad. 3 calves	5.0

[a]Includes an estimated 318 kg from a necropsied bull.
[b]Includes an estimated 286 kg from a necropsied cow.
[c]Includes an estimated 368 kg from a necropsied cow and calf.

Food available to pack members from 1971 through 1973 on Isle Royale was greater than that indicated for the former large pack (Mech 1966). Using the moose weights given above, that pack had available 4.9, 3.8, and 5.1 kg/wolf/day in 1959, 1960, and 1961, respectively.

Food available to Isle Royale wolves is well above the minimum amount required in winter. Mech (1970) estimated the daily food requirement for a wild wolf at about 1.7 kg on the basis that active domestic dogs need about this amount. Growing wolf pups and captive adults can be maintained on this amount of food (Kuyt 1972; Mech 1970). Food availability for an Ontario wolf pack was estimated at 3.7 kg/wolf/day during one winter season (Kolenosky 1972). A Minnesota wolf pack increased after a winter with 5.8 kg/wolf/day of available food, remained the same size at 3.6 kg/wolf/day, and decreased at 3.4 and 3.0 kg/wolf/day (Mech, in press).

The food economy of loners (single wolves) and small groups is difficult to study because the extent of their movements and feeding patterns is usually unknown. Although Jordan et al. (1967) described some loners as "gaunt" and implied that most led a rather tenuous existence, this may not be the case in winters of abundant prey. For example, in 1971 a loner subsisted for several weeks on three moose carcasses in the Malone Bay area and apparently moved very little. Likewise, the Todd duo killed two moose and fed on two old kills in a 15-day period in February 1974, rarely moving out of the Todd Harbor area.

Long-term Changes in Food Resources

The appearance of two socially stable wolf packs on Isle Royale was not observed prior to 1972; this appearance, presented earlier, probably resulted from an increase in the food base of the wolf population. The beaver population increased in the 1960s, as did wolf predation on beaver during the nonwinter months. Since production of moose calves was noticeably lower in recent years than in the early 1960s, beaver assumed a position of significance by supplying food during the critical pup-rearing season.

While the moose population also appeared to increase during the 1960s, this would not in itself provide an immediate increase in prey for wolves. The food supply for wolves depends on the density of vulnerable moose rather than absolute moose densities. Thus, a moose population in the early stages of a natural decline may provide wolves with a maximum number of available prey. This was apparently the case on Isle Royale in the early 1970s.

The establishment of the East Pack has probably brought about a greater utilization of prey within this territory, where previously only loners or packs of two or three wolves lived. For example, the number of moose killed on the northeast half of the island during the winter study period increased greatly from 1971 to 1972, after the appearance of the East Pack (Fig. 47). In its first three winters of operation, the pack killed nine moose on the Blake Point peninsula, about 8.5 km^2 in area, during a total of 18 weeks of aerial tracking. Ground search

turned up eight additional kills on this peninsula. Moose densities in midwinter in this area commonly exceed 4–6/km².

Intraspecific Behavior

Like physical characteristics, an animal's behavior has been shaped by rigorous selection pressures, resulting in behavior patterns that are closely adapted to a particular function in the ecosystem. A comparison of the red fox and wolf provides a simple illustration. While both are canids, foxes exhibit much less diversity in behavioral expression and communication than do wolves (Fox 1970). The fox, a semi-solitary creature, preys extensively on game smaller than itself and, at certain seasons, depends heavily on plant fruits and carrion. Therefore, in terms of food acquisition, there would be no advantage for young foxes to remain with their parents in a social group. The behavioral repertoire of foxes is less diverse, yet sufficient for its more solitary way of life. Cooperation among wolves in a pack, however, is essential to their ecological role as a predator on large ungulates. Consequently a complex dominance hierarchy and elaborate array of behavioral expression have evolved among wolves, allowing them to live in close association as group-hunting carnivores.

The organization of wolf populations into packs does not fully explain wolves' diverse means of expression and communication, since other group-hunting canids, notably the bush dog (*Speothos venaticus*) of South America and the African wild dog (*Lycaon pictus*), do not exhibit a similar, high level of behavioral expression (Fox 1971; Kruuk 1972). While little is known of the ecology of the bush dog, the wild dog of Africa exists year-round in a cohesive pack, with social bonds apparently maintained by highly ritualized food-begging behavior (Kühme 1965). Individuals within a wolf pack are frequently separate, however, especially in summer when most hunting is done individually or in small groups. This led Fox (1971) and Kruuk (1972) to suggest that the well-developed means of expression among wolves is not only important in coordinating group activities and maintaining order in the pack but also provides for more effective reintegration of individuals into the group after separation.

The territorial nature of wolf packs helps maintain pack integrity and seems to apportion space among resident packs according to the availability of food. Mechanisms of territory maintenance may include scent-marking and howling and agonistic behavior during rare confrontations between packs.

In spite of extensive field studies of the wolf, many generalizations concerning behavior within and between packs are poorly documented in the wild, primarily because observations are hampered by the wolf's environment and mobility. Lengthy ground observations have been possible only at den sites in tundra regions (Murie 1944; Haber 1968; Clark 1971); aerial observations, a primary research

tool, are limited in scope. Insight into the ecological significance of wolf behavior patterns and a proper appreciation of their variability can be gained only by intensive study of many packs in different ecological settings.

Social Hierarchy Within Packs

The basic social structure of wolf packs is well understood from studies of captive wolves (Schenkel 1947, 1967; Rabb et al. 1967). Behavioral interaction within a pack occurs in a framework of dominance relationships or social hierarchy. A dominant (or alpha) male and female are the central members of a pack, and the other wolves constantly reaffirm their subordinate status through postures of submission directed toward the dominant individuals. Males and females have a separate dominance ranking, and the subordinates have definite dominance relationships among themselves, although interaction is less frequent and relationships are less well defined.

Aggression is channeled into ritualized behavior patterns within the dominance framework, reducing the amount of direct conflict within the pack and promoting social order and stability. Alpha wolves provide leadership during travels of the pack, initiate many pack activities, and sometimes exert considerable social control over activities of subordinate wolves, notably their sexual behavior.

Restriction of courtship behavior among subordinates, together with well-developed mate preferences among adults, is thought to reduce the potential number of breeding pairs in a pack, often resulting in the birth of only a single litter. The whole pack participates in gathering food and caring for the young, and this contributes both to the survival of young and cohesion within the pack.

EXPRESSION OF DOMINANCE AND SUBORDINATION

Facial expression, tail position, and posture combine to indicate subtleties of mood and desire. These indicators provided the basis for determining the social position of certain wolves in the packs on Isle Royale, especially the alpha wolves (Fig. 48).

Tail position is easily seen from the air and is thus an obvious indicator of wolf status. The importance of the tail in communication probably lies in the fact that the hindquarters and anogenital region have a considerable function in olfactory and visual expression (Kleiman 1967; Schenkel 1947). Presentation of the anal region by a raised tail indicates a position of dominance, while a lowered tail (during interaction with other wolves) covering the anal region, is a component of submissive behavior. Postural changes reinforce these expressions: a dominant wolf stands erect with tail raised, while an extremely subordinate animal may pull its tail between its legs and lower its rear end to the ground (Figs. 49, 50).

While the movements and positions of the ears, eyes, forehead, nose, and mouth of a wolf can be combined to produce subtle variations of expressions (Schenkel 1947), most are not observed by humans except at close range. Ears of dominant

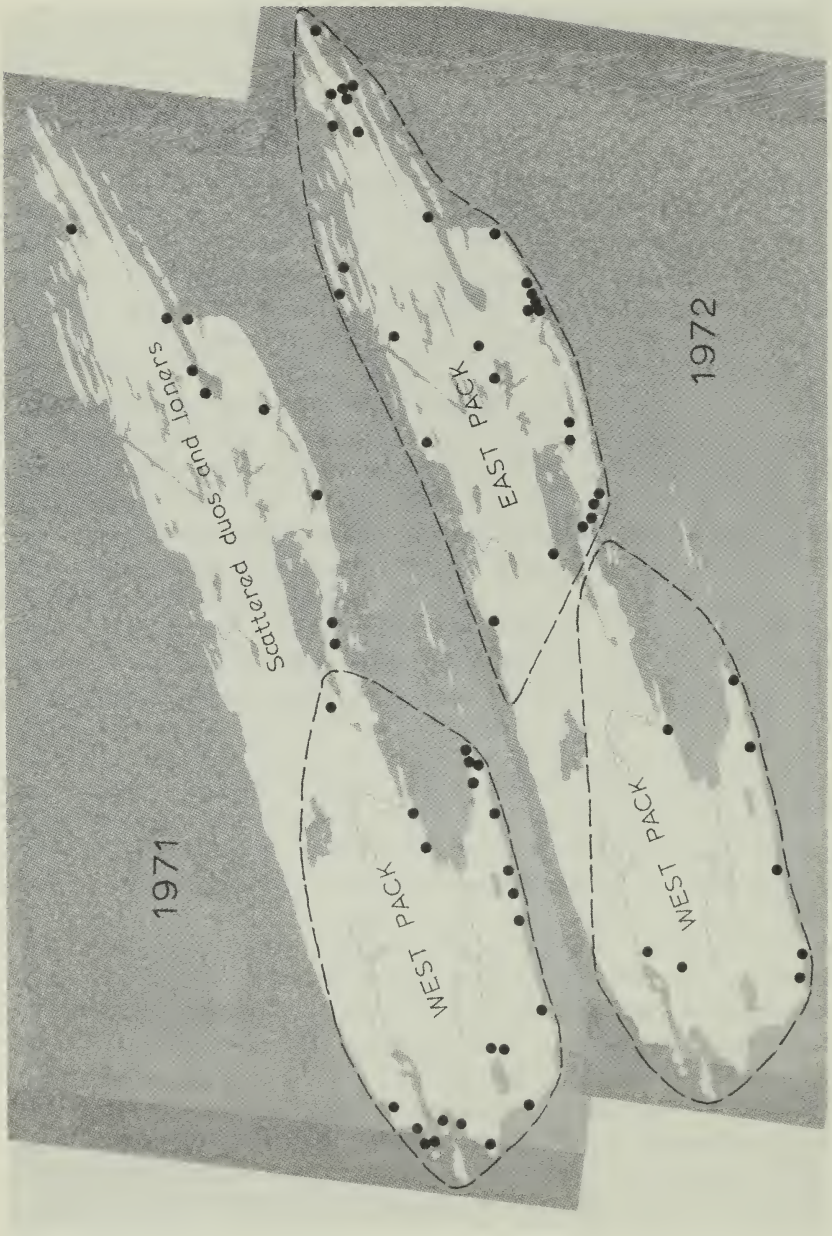


Fig. 47. Distribution of wolf kills located during winter study before (1971) and after (1972) the establishment of the East Pack.

Fig. 48. Alpha female and male lead West Pack, 1972. Note raised tails of dominant wolves.

wolves are forward, while those of subordinate wolves are turned back or flattened against the head. Teeth are more exposed as the intensity of a threat increases. Wolves of high social standing often stare directly at another wolf as part of an expression of dominance or a mild threat, and subordinates respond by turning the head away and avoiding direct eye contact.

Inferior wolves constantly show submissive behavior toward dominant wolves. Schenkel (1967:324) defined submission as "an impulse and effort of the inferior towards friendly and harmonic social integration." He described two basic types of submission in wolves, "active" and "passive." During active submission,

> . . . the posture is slightly crouched, the tail is low, and the ears are directed backwards and lie close to the head. . . . The inferior pushes the muzzle of the superior with his nose, licking it tenderly without any pressure, In addition, he may perform pawing movements—lifting one forepaw and moving it in the direction of the superior, or, while making little steps, tapping the floor with his forepaws alternately. Often the tail is wagging sideways, and sometimes the whole hindquarters are also swinging. (Schenkel 1967:322–323).

Active submission often is seen as an element in greeting behavior, and is the most obvious form of expression during the "group ceremony," described below. Passive submission is usually shown by an inferior wolf in response to a threat from a superior individual:

> The inferior wolf lies half on his side and half on his back, exposing the ventral side of his chest and sometimes the abdomen. The latter occurs regularly as a reaction to olfactory investigation in the genital region. The ears are directed backwards and lie close to the

Fig. 49. Alpha female (Brookfield Zoo) follows subordinate female. Note posture and head and tail position.

Fig. 50. Alpha male (East Pack, 1974) stands in dominant display next to subordinate wolf.

> head. The tail is more or less bent ventrally so that it passes between the thighs. The often enthusiastic and friendly activity of active submission is reduced. Sometimes the tail is wagging sideways with extremely reduced amplitude and the activity is replaced by a passive posture full of trust, devotion, and demonstrated helplessness (Schenkel 1967:323).

An important element in passive submission is "inguinal presentation," in which the wolf lying on its side raises its hind leg, thus exposing its inguinal region to the dominant wolf. Passive submission, and inguinal presentation in particular, seem to inhibit aggression in dominant wolves and thus are considered appeasement or "cut-off" gestures (Fox 1971). Many times on Isle Royale, active agonistic behavior, or even mild threats, from a dominant wolf caused subordinate individuals to fall into passive submission. The dominant wolf usually would reduce the level of its threat, and either investigate the prone wolf or simply stand over it for a minute or more. Slight movement by the inferior wolf usually brought a quick snap from the dominant. The subordinate wolf usually lay still, often with hind leg raised, until the dominant wolf walked off. Once, in the West Pack, a subordinate wolf maintained a position of inguinal presentation after the black alpha male walked away, and even rolled over and raised the other hind leg when the alpha male wandered behind him. Any other movement by the inferior male brought immediate punishment from the alpha male.

Members of a pack often congregate in a "group ceremony," a greeting centered around the alpha animals. Subordinates crowd around the dominant wolves and show exuberant active submission and much body contact. Group ceremonies were observed 34 times among Isle Royale wolves from 1972 to 1974. Most commonly, they occurred immediately after the pack arose from sleep, or when one or several members returned to the pack after a brief absence. Frequently active submission toward an alpha by one wolf brought the rest of the pack running over to join in the proceedings, and sometimes a group ceremony ensued when wolves clustered about an alpha inspecting an inferior wolf lying on the ground. Group ceremonies also were seen when a pack "regrouped" after an unsuccessful chase of a moose. Such ceremonies often terminated with threats directed toward an inferior wolf by an alpha, perhaps in response to overenthusiastic greeting behavior. Group ceremonies provide a means of reaffirming dominance relationships, probably reinforcing both the status of alpha wolves and existing social bonds. Additionally, they may provide reassurance for pack members at critical periods; for example, when the East Pack traveled outside of its normal territory in 1974, subordinate wolves constantly crowded about the alpha wolves in a group greeting.

PACK LEADERSHIP

Alpha wolves sometimes retain their dominant position for several years and may be instrumental in maintaining a stable pack. Jordan et al. (1967) recognized the alpha male in the large pack on Isle Royale from 1964 to 1966 and found that pack

formation in 1966 coincided with his death. There has been relatively little turnover in the alpha positions in the West and East packs (Fig. 51). The small, gray female with the deformed left front leg held the alpha position for at least 5 years (1968–72) in the Big Pack (West Pack). The black male was associated with this female during all 5 years, apparently first as a subordinate (beta) male with special privileges allowing him to travel and rest near the alpha pair (Wolfe and Allen 1973), and finally as alpha male in 1971 and 1972. This was the only case from Isle Royale in which the previous history of an alpha animal has been known.

None of the recognizable alpha wolves on Isle Royale has been seen after a known change in its dominant status, but whether their deaths preceded or followed the change in leadership is unknown. Jordan et al. (1967) found circumstantial evidence that the alpha male in the large pack in 1966 had been killed by his associates. During the present study, three alpha wolves disappeared; all three were last seen in summer. While the alpha male in 1966 apparently was killed after he developed a limp, the alpha female in the West Pack in 1972 managed to maintain her dominant status in spite of a limp which occasionally prevented her from retaining her customary position at the front of the pack.

Winter observations on Isle Royale indicated that alpha wolves usually led the pack during its travels. Of 61 cases in which it was possible to determine whether the alpha male or female led the pack, an alpha wolf was first in line 70% ($n = 43$) of the time. In 33 cases the alpha female was first, the alpha male led in 6 cases, and 4 times the two dominant wolves were side by side. In many instances the alpha male showed obvious sexual interest in the alpha female and consequently followed her.

Alpha wolves, usually at the front of the pack, normally choose the direction of travel and specific travel routes. This clearly was the case during an observation of the East Pack in 1974. The alpha female led the pack through the narrows between Wood Lake and Siskiwit Lake, then lagged behind to sniff an old moose track. Other wolves then assumed the lead position until they reached the first peninsula, where they stopped and waited for the alpha female to move to the front. She immediately set the direction of travel, led the way briefly, then fell back into a position in the middle of the pack. The same procedure was followed at the next point of land.

A clear example of decision-making on the part of an alpha animal was observed in 1974 when the East Pack encountered a scent post of the West Pack. After the pack had examined the scent mark, the alpha female reversed the direction of travel and led the pack back to more familiar range.

In the absence of alpha leadership, subordinate wolves may be indecisive. Once in 1972 we observed six probable pups in the East Pack by themselves when the alpha pair had dropped back several miles. Twice a wolf stopped and watched its back-trail. When the six wolves emerged on the shore of an inland lake, they vacillated for 15 minutes, sniffing snowed-in tracks and making false starts, and finally all started off in the same direction.

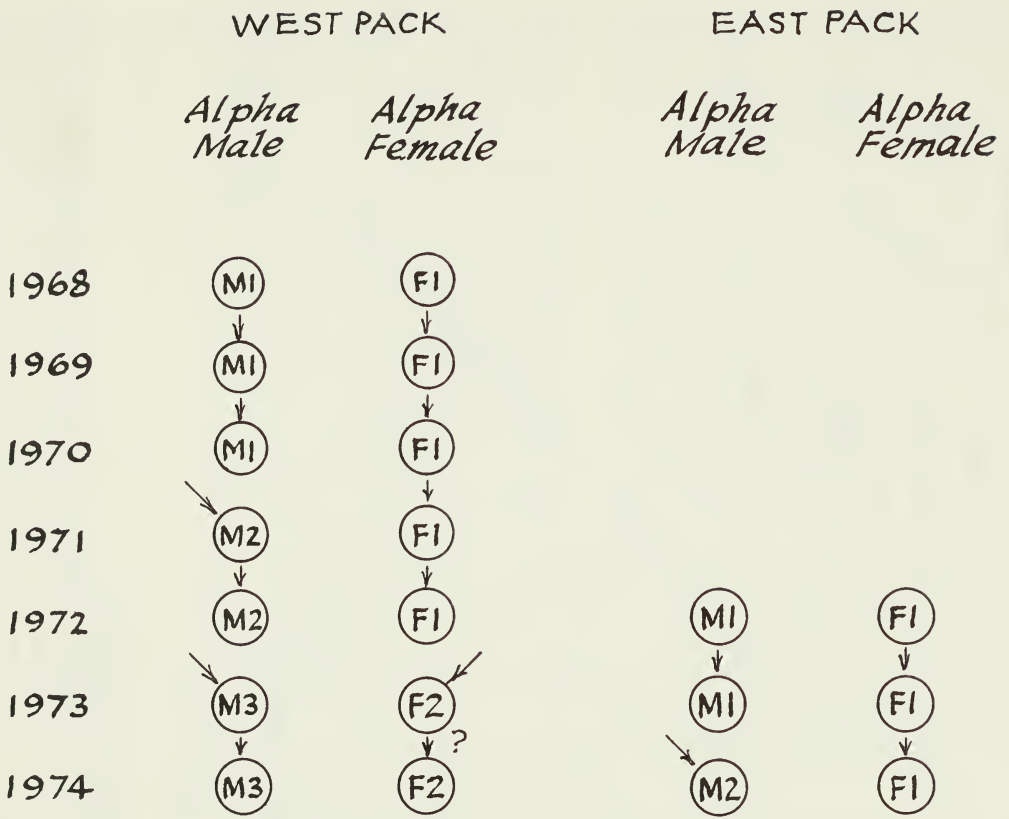


Fig. 51. Changes in leadership of the large packs on Isle Royale.

Alpha wolves appear to provide leadership at critical times such as hunting, encountering novel stimuli, and perhaps when contacting neighboring packs. The position of the alpha wolves was observed in only six encounters with moose, but an alpha wolf led the pack in four of these cases. Certainly the wolves at the front of a pack would be the first to detect and chase prey.

In February 1973, when the West Pack was under observation at a moose carcass across the harbor from Windigo, the alpha male detected us. He trotted excitedly toward shore, then back to arouse other members of the pack. After a group ceremony centered around him, he led the pack into thick cover near shore.

Later in the same winter we watched the East Pack file along the ice on the north shore of Rock Harbor. When they reached open water, they moved onshore and slowly worked their way long the slippery, ice-coated shoreline, finally congregating on a small point. Rounded chunks of broken, "pancake" ice ranging up to several feet in diameter had frozen loosely together adjacent to the point. One wolf reached out with a foot and pushed on an ice chunk, withdrawing its foot quickly. Next the alpha male, together with an unidentified wolf, walked out on a large chunk of ice and stood for a few seconds. Suddenly they bolted back to shore, apparently after the ice had shifted. The alpha male then led the pack away, continuing the course onshore.

No observations were made of confrontations between different packs of wolves on Isle Royale. However, we might expect that the alpha animals would take a leading role in such a situation, much as they did when an alpha wolf led the pack in chasing a fox in two observed cases. Although the alpha male and female did not lead the East Pack during their first foray out of their territory on 15 February 1974, they were obviously key figures. As the pack ventured across Siskiwit Bay, most of these wolves probably were encountering the area for the first time, since this pack was not observed southwest of Malone Bay in the previous two winters. In addition to an unusual amount of scent-marking as they crossed to Houghton Point, the subordinate wolves were constantly clustered around the dominant pair in a sort of mobile group ceremony. Perhaps the intense, active submission directed toward the alpha pair resulted from uncertainty and excitement among subordinate wolves.

Courtship and Breeding

Largely because of complex social relationships, such as mate preferences and a dominance hierarchy, the breeding potential of a wolf pack rarely is realized. Studies of captive wolves have demonstrated that breeding within a pack usually is limited to a few animals (Rabb et al. 1967), and a similar situation has been observed in packs on Isle Royale. In studying wild wolves, it should be remembered that sexually immature pups may account for a sizable proportion of a pack, a partial explanation for limited breeding activity.

Mate preferences are recognized clearly on Isle Royale, and incidence of courtship among Isle Royale wolves indicates that mating is most likely to occur

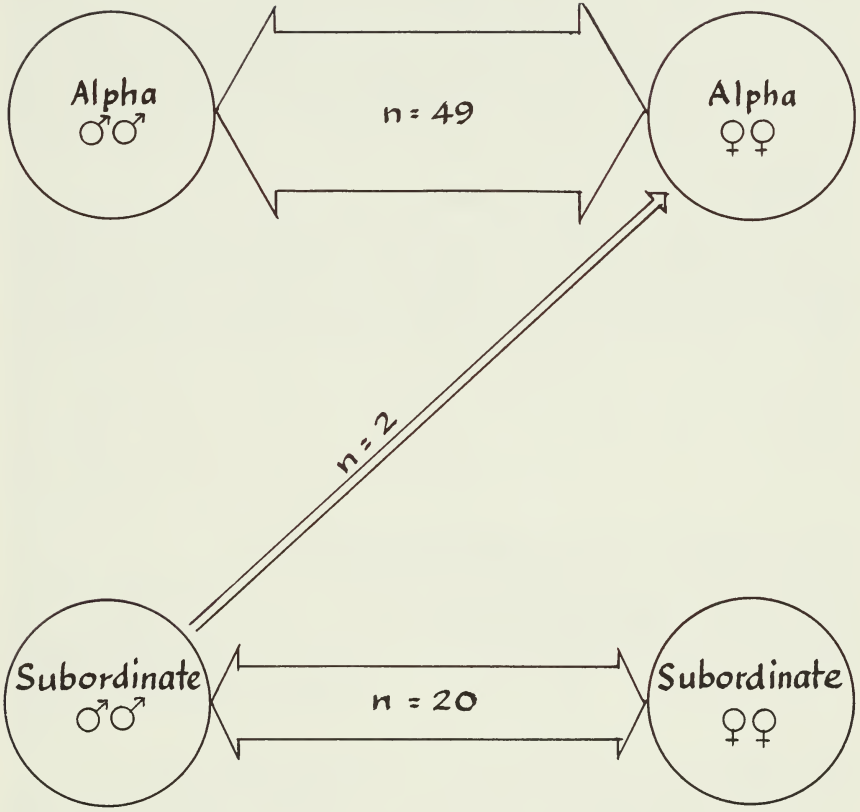


Fig. 52. Incidence of courtship behavior between wolves of different social rank in the East and West packs on Isle Royale, 1972-74.

between the dominant male and female in a pack (Fig. 52, Table 11). It is also obvious that alpha wolves interfere with courtship attempts of subordinates. These topics will be presented in depth later in this section.

The primary function of courtship behavior is to establish and maintain a pair bond. Unlike many vertebrates, male wolves play an integral role in feeding and raising the pups, and a close relationship between a male and female wolf remains important on a year-round basis. Although there are records of more than one litter born in a pack (Murie 1944; Haber 1968; Clark 1971), one litter per pack is usually the rule (Van Ballenberghe and Mech 1975) and probably a safe assumption when pack sizes are not large. Other adults in a pack help raise the pups, enhancing their chances of survival. On this basis we can predict that natural selection would favor offspring from dominant, breeding wolves that interfered with mating attempts of subordinates in a pack.

In species with well-developed threat behavior, such expressions are well hidden during courtship, since they would be detrimental to the formation of a close relationship between male and female (Eibl-Eibesfeldt 1970). Consequently, courting wolves display much greeting behavior, play soliciting, and submissive postures, all of which tend to decrease "social distance" (Fox 1971) (Fig. 53).

TABLE 11. Minimum number of breeding pairs present, 1971–74.

Year	Estimated minimum number of breeding pairs	Remarks
1971	2	Alpha pair, West Pack,[a] 7, 8 Feb. Progenitors of East Pack
1972	3	Alpha pair, West Pack Alpha pair, East Pack Subordinate pair, West Pack,[a] 2 Mar.
1973	2	Alpha pair, West Pack,[a] 16 Feb. Alpha pair, East Pack (Todd duo ??)
1974	4	Alpha pair, West Pack Alpha pair, East Pack Subordinate pair, West Pack,[a] 4 Feb. Todd duo

[a]Mating observed. In the other cases mutual courtship indicated the strong likelihood of mating. A second breeding pair in 1971 is inferred from the establishment of the East Pack.

Courtship behavior was observed among Isle Royale wolves throughout the annual winter study periods, with the peak in sexual activity usually sometime in February. During 52 hours of aerial and ground observation in winters from 1972 through 1974, courtship behavior was recorded 71 times. One "instance" of courtship behavior consisted of a well-defined behavior or sequence of behavior, such as mounting, a mutual greeting between mates, etc. Behavior patterns which were considered as courtship in at least some contexts are described in Appendix F. Most of the courtship behavior recorded consisted of males mounting females or males examining the genital region of females (genital snuffling). Undoubtedly, these behaviors are somewhat overrepresented because they are so easily recognized. Greeting and play behavior were also commonly seen but were not recorded as courtship unless there were other indications of sexual interest.

Subtleties of behavioral expression are not seen readily from aircraft. When observing wolves whose sex, age, and relationships are unknown or poorly understood, some ambiguous behavior is difficult to classify. For example, it was not uncommon to see one wolf approach another with tail flagged, posture erect, ears and eyes forward, and the second wolf walk off in a generally submissive posture, tail tucked between its legs. This usually indicated a dominance display, but similar behavior was seen when a male tried to court an uncooperative female. Such ambiguities were resolved by carefully watching for subsequent interaction between the same individuals and their relationships to other wolves. Fortunately, most displays of dominance, submission, and courtship involved recognizable alpha wolves and were interpreted with little difficulty.

MATE PREFERENCE

Mate preference can be a powerful limitation on the amount of breeding within a pack. Clearly, if there is no mutual courtship between a male and female wolf, a mating between the two is unlikely. The breeding potential of the Brookfield wolves was reduced considerably by such "one-sided" courtships (Rabb et al. 1967).

Pair bonds between mates may be very stable from year to year, although wolves will mate with other individuals if their preferred mate is not available (Rabb et al. 1967). Wolfe and Allen (1973) indicated a stable pair bond between the alpha male and female in the Big Pack (West Pack) from 1968 through 1970. This male had disappeared by 1971, but the same female mated in 1971, and presumably in 1972, with the black male that assumed the alpha position. The East Pack provided another example of a female accepting a new mate after the probable death of the alpha male. In 1974 the new alpha male courted the incumbent alpha female, who accepted his approaches with friendly greetings, indicating probable receptiveness. In all the packs observed from 1971 through 1974, the alpha pair either mated or showed mutual courtship and was considered a bonded pair.

Studies of the Brookfield wolves (Rabb et al. 1967) showed that both males and females sometimes courted members of the opposite sex that were unreceptive,

Fig. 53. Play behavior is an integral part of wolf courtship (Brookfield Zoo).

Fig. 54. Female accepting a courting male (Brookfield Zoo).

Fig. 55. Female rejecting a courting male (Brookfield Zoo).

and in these cases courtship action was ignored or rebuffed with threats (Figs. 54, 55). My own observations at Brookfield indicated clear differences between the behavior of females that simply were not ready for copulation and those that were totally rejecting a male. A female that temporarily was rejecting a male responded to his advances with mild threats, or simply pulled away, and elements of greeting and play behavior were still seen between partners. This was typically the situation between alpha males and females on Isle Royale, and also a subordinate pair in the West Pack in 1972 that eventually mated. However, a female that was unreceptive to a particular male responded to his courtship attempts with obvious threats and showed little friendly behavior, except perhaps in the context of a group greeting ceremony. A subordinate male in the West Pack in 1973 frequently showed interest in a female, but she always replied with aggressive snapping, never exhibiting any friendly behavior toward the male. A mating between these wolves seemed unlikely.

Little is known of the development of mate preferences among wild wolves, but among Brookfield wolves there were strong indications that future mate preferences are crystallized during the juvenile period (prior to sexual maturity at 22 months). Also, it appears that a young wolf generally develops a preference for the alpha wolf of the opposite sex, or at least a dominant individual (Rabb et al. 1967; Woolpy 1968). It is significant that the alpha female in the West Pack in 1971 accepted the black male as her new mate—a wolf that had enjoyed a close relationship with the alpha pair for at least 3 years.

RESTRICTION OF SEXUAL BEHAVIOR AMONG SUBORDINATE WOLVES

During three breeding seasons on Isle Royale, 69% of the observed courtship behavior ($n = 71$) occurred between alpha wolves. Studies of captive wolves have shown that dominant wolves restrict and, in some cases, eliminate courtship behavior and mating among subordinates (Schenkel 1947; Rabb et al. 1967; Woolpy 1968). Since the reduction of mating among subordinate adults could contribute to population regulation, it is important to try to determine the effectiveness of such restrictions among wild wolves.

Rabb et al. (1967) noted an increase in agonistic behavior between dominants and subordinates during the breeding season of Brookfield wolves (Fig. 56). Observations in February on Isle Royale indicated frequent threats to subordinate wolves by the alpha male and female. In many cases a strong assertion of dominance seemed to be stimulated directly by courtship behavior among subordinates. This was further indicated by the lack of overt threats from the alpha male in the East Pack in 1972, when the pack was believed to consist primarily of an alpha pair and their offspring; the latter would have been sexually immature in their first winter. In 1973, however, when pups of the previous year could have been sexually mature, on two occasions the alpha male chased other wolves away from the alpha female. Both instances occurred on 16 February when frequent genital sniffing by the alpha male suggested that his mate was in heat.

The West Pack provided the best opportunity to record interference of alpha wolves in the sexual behavior of subordinates. The black alpha male in this pack was very possessive of his mate, the alpha female of long standing (Fig. 57). One of my first observations of this pack was from the ground at Windigo on 29 January, 1972. As they rounded Beaver Island, there was much playful sparring as the pack moved along the ice, and at one point a subordinate wolf mounted the alpha female. She eventually squirmed away and snapped at the other wolf, and this brought the black male on a run. He knocked the subordinate over with a body slam, and then mounted the alpha female himself. This was typical of his behavior when other wolves approached his mate.

The most interesting interaction in 1972 spanned several days, beginning 24 February. A subordinate pair managed to stay in the West Pack and mate in the presence of the alpha pair, in spite of repeated punishment from both the alpha male and female. Identification of the subordinate pair was not always positive: the male was a thin-tailed wolf that looked like one other wolf in the pack, and the female was one of three full-tailed wolves in the pack. This complicated the interpretation of observations made at different times, but since there was never any indication of sexual interest in more than two subordinate wolves, in the following account from my field notes, it will be assumed that the thin-tailed male and the full-tailed female were consistently the same individuals.

> February 24: The West Pack (seven wolves) was traveling southwest along the shoreline of the island opposite L. Halloran at 5:15 p.m., when we began observations.

Fig. 56. Alpha male attacking (with inhibited bites) a subordinate male mounting a female (Brookfield Zoo).

Fig. 57. Black alpha male stands between alpha female (behind him) and subordinate male (head turned away), West Pack, 1972.

The alpha female was limping very noticeably and had fallen to the rear of the pack, accompanied by the alpha male. The full-tailed female assumed the lead position for most of the observation period of 45 minutes. Once she squatted and urinated on the ice, and the alpha female accompanied by her mate, walked over and inspected the urine mark. The other wolves crowded around and likewise sniffed the spot. Then the full-tailed female joined the group and, when approached by the alpha female, immediately dropped on her side in passive submission. The alpha female went back to the urine mark for an additional sniff, and the full-tailed female arose, only to be forced back down on her side by the alpha female. When the pack began to move on, the full-tailed female again assumed the lead position, the alpha pair falling to the rear. Since the alpha female was almost always in the front of this pack when it traveled, it appeared that the full-tailed female might have been punished for assuming the lead position. Perhaps the urine mark of the female indicated an estrous condition, which might have precipitated the punishment. We followed for another 30 minutes as they encountered several moose along the shore, finally killing a calf.

February 26: The pack (seven) left the kill made 2 days earlier and traveled around the western end of the island. We watched them from 4:20 p.m. to 5:40 p.m. as they rounded the western-most point of land and entered Washington Harbor. In the first 55 minutes of observation, the alpha female "punished" the full-tailed female four times, forcing her over on her side. During this time the thin-tailed male sniffed the genital region of the full-tailed wolf, and they engaged in a brief nose-greeting as they traveled. The wolves were spread out on the ice, with the subordinate pair usually in the front and the alpha pair near the center. At the mouth of Washington Harbor, the thin-tailed male mounted the full-tailed female briefly, causing the alpha pair and the rest of the pack to run over. After the alpha female "punished" the full-tailed female their identification became uncertain in the flurry of activity which ensued. Suddenly four subordinate wolves, including the full-tailed female, broke from the group and ran toward Card Point, 300 m to the south, pursued by the alpha pair. Three of the four wolves stopped when they reached the point, but the full-tailed female ran across the point, around its western end, and then doubled back across the mouth of Washington Harbor. The alpha pair joined the three wolves on the shore of Card Point briefly, but when the full-tailed female came into view, the alpha female took off on a run after her, accompanied by her mate, the black male. The rest of the wolves joined half-heartedly in the chase. The full-tailed female maintained a long lead on the alpha pair, however, and after running across the point on the north side of the mouth of Washington Harbor, the alpha pair and the rest of the pack slowed to walk. They continued to track the full-tailed female, who after running 4.0 km, was still trotting, with frequent glances over her shoulder, when darkness forced us to terminate observations.

February 27: Six wolves were observed near the carcass of a moose near Windigo. The alpha pair and two others walked out of view onto shore, leaving a thin-tailed wolf standing near the carcass and a full-tailed female feeding voraciously on the remaining bones, suggesting a late arrival. It seemed reasonable that this was the subordinate pair, since the thin-tailed wolf pawed and sniffed at the genital region of the full-tailed wolf after the others had left. The pack still was missing one wolf.

February 29: The pack had traveled 37 km to Houghton Point, where they killed a moose and were seen in early afternoon resting nearby. Only six wolves were seen, and only the alpha pair was identified.

March 2: In the afternoon all seven wolves of the West Pack entered Washington Harbor, on their way to the bait carcass. The full-tailed female and thin-tailed male led the

pack, traveling close together. At 6:00 p.m. the wolves arrived at the carcass, which was covered with snow. The thin-tailed male and full-tailed female remained close together, often playfully chasing one another. Once, as this pair came romping toward the carcass, the male sniffed her rear end while in view of the alpha pair. The black alpha male raised his tail and stared at them, and the alpha female walked stiffly toward the full-tailed female, forced her into passive submission, and nipped at her neck as she lay on the ice. The subordinate pair walked a short distance away from the carcass and things quieted down. For approximately the next hour the wolves either rested quietly on the ice or chewed on the remaining bones.

At 7:15 p.m., apparently with no preliminaries, the thin-tailed male mounted and "tied" with the full-tailed female. The male swung one leg over the back of the female 35 seconds later, and they stood back to back. The alpha pair immediately ran over to the tied pair, who then dropped to the ice on their sides, still tied. The black male stayed for only a few seconds, nipping at the male and probably threatening, and then returned to feed on the carcass. The alpha female bit at the neck of the prostrate female many times, then stood over the pair for the next 2 minutes. Another wolf came to watch the proceedings, and the black male made another brief visit. The alpha female continued to stare at the tied female, her upright tail slowly moving back and forth. Five minutes and 50 seconds after tying, the pair uncoupled, and the alpha female responded with a brief "punishing" sequence, consisting primarily of nips directed at the still-prone female. Then the alpha female headed back to the carcass, and the subordinate pair ran together, nose-greeting each other, wagging their tails and occasionally standing on their hind legs with front limbs entwined. Three minutes later they joined the other wolves on the carcass, passing the alpha female with no overt threatening gestures from the latter.

March 3: West Pack (seven) still near the carcass, with only the full-tailed female that mated actually feeding. Her mate inspected her genital region several times with the alpha pair nearby, but stimulated no visible threat from them. When they rested, they lay together, just as the alpha pair did.

March 9: The pack was observed for the final time in late afternoon—seven wolves traveling along the north shore of the island. A thin-tailed wolf trotted close behind a full-tailed wolf, and there was no observed interaction between the alpha pair and the other wolves.

Significant in these observations was the very aggressive attitude of the alpha female toward the full-tailed female when she was courting the thin-tailed male. Having been chased from the pack, however, the subordinate female managed to reinstate herself and mate successfully in spite of her "punishment." The black male usually did not interfere with the subordinate male's courtship activities and showed brief aggression only when the subordinate pair actually tied. In this case the discouraging influence of the alpha pair was not sufficient to prevent mating of subordinates, although the length of their copulatory tie was shorter than normal.

A subordinate pair was present in the West Pack in 1973, and the alpha pair actively interfered with their courtship activities. On 6 February they were observed near a carcass at Windigo:

> The subordinate (long-tailed) male continued to show an interest in the subordinate female, who rebuffed him each time. Twice the alpha male reacted to the courtship attempts of the subordinate male with threats and inhibited bites to the head and scruff,

usually after the latter had dropped on his side in passive submission. Each time, however, the long-tailed male lay on the ice until the alpha had left the immediate area, then resumed courting the subordinate female. Finally both the alpha male and female approached the subordinate pair, and each threatened the subordinate of its respective sex. The alpha wolves stood over them as they assumed a position of passive submission. After inhibited biting of the prostrate male, the alpha male walked over to the subordinate female and evidently bit her—her yelp was clearly heard at our observation post 0.8 km away.

While the efforts of the alpha pair to discourage courtship in this subordinate pair were persistent, of greater importance was the subordinate female's apparently irreversible lack of interest in the advances of the male.

Before the West Pack fragmented in early February 1974, a presumably subordinate pair was observed mating while the pack rested nearby. The status of the alpha male from 1973 was not established before the mating took place, and immediately afterwards he behaved in a very subdued manner, walking at the rear of the pack with his tail down, while the mating pair led the way. This suggested a change in his status, yet he was still the alpha wolf in both the group of four in which he was later found and the pack of eight that reformed in early March.

From the above accounts, it is obvious that alpha wolves usually interfere with attempts at courtship among subordinate wolves, although I did not record a case when they were actually able to prevent mating among subordinates. Such behavior on the part of the alpha wolves may, however, discourage pair-bond formation or initial sexual interest among subordinates. In the wild, of course, a subordinate pair could leave a pack and breed with no disturbance, but in such a case reintegration into the pack might be difficult.

Our understanding of the effect of the dominance hierarchy on the formation of breeding pairs within a pack is still inadequate. In several packs, both captive and wild, the alpha male did not father the pups, or was relatively inactive sexually (Murie 1944; Rabb et al. 1967; Haber 1968). In the Brookfield pack, a male reduced his participation in courtship activities after assuming the alpha position. However, alpha wolves in both the East Pack and West Pack on Isle Royale have exhibited the most courtship behavior. Individual personalities and attributes and filial or allegiance bonds among wolves can greatly alter relationships within a pack (Rabb et al. 1967) and ultimately will limit the degree to which we can generalize about mate preference and the restriction of breeding among subordinate wolves.

IMPLICATIONS OF SOCIALLY CONTROLLED MATING

Behavioral limitations on mating, including mate preferences, may hold the productivity of wolves considerably below the theoretical maximum, and often only one litter of pups is born, even in large packs. The food-gathering abilities of the adults in the pack then contribute to the growth of a relatively small number of pups, enhancing their chances of survival.

Since packs are basically family groups, there is obviously a high potential for inbreeding in stable packs. Woolpy (1968) studied the genetic implications of social organization in wolves. He contended that the notion that inbreeding results in deleterious effects probably is of little significance when genes are naturally "preselected" for combinations of adaptive value, as they are in wolves. As a demonstration of this principle he cited a study by Scott and Fuller (1965), who inbred beagles and basenjis with no deleterious effects, after preselecting them for fertility, behavior, and body conformation. We have already seen that the parents of wolf pups in the wild are likely to be dominant wolves, already preselected for traits of leadership and physical attributes (Fox and Andrews 1972). Of course, natural selection will rapidly eliminate inferior pups born in the wild.

Woolpy (1968) further concluded that the organization of wolf populations into discrete packs, or subpopulations, was of considerable evolutionary significance. According to his hypothesis, over a period of several years of strong leadership in which most pups are born to a single pair, the expression of available genotypes (gene combinations) within a pack will be greatly reduced. Simultaneously, because of inbreeding, viable recessive gene combinations will appear more frequently. In the long run, this could result in greater variability between wolf packs. Thus, several genetic "lines" of wolves are maintained, with genetic variability partitioned "to give maximum exposure (to recessive gene combinations) at all times and to allow them to compete with each other and thus . . . provide the potential to move the population to new adaptive phenotypes" (Woolpy 1968:32). In a sense, due to wolves' social organization, evolution of the species would be accelerated, resulting in rapid adaptation to different environments. Such adaptability is evidenced by the original widespread distribution of wolves in North America and the description of 23 original subspecies on this continent (Goldman 1944). A major challenge facing us today is whether we can preserve a sufficiently large number of natural ecosystems to allow wolves and other species to achieve their own evolutionary potential.

Territoriality

In spite of extensive field studies of wolves in various parts of North America, the precise nature of spatial relationships between adjacent packs was unknown until recently. It was unclear whether wolf packs occupied exclusive, nonoverlapping territories or whether neighboring packs utilized common hunting grounds, simply avoiding each other through direct and indirect communication.

Recent studies of radio-marked wolves in many packs in Minnesota helped crystallize a concept of "land tenure" among wolf packs (Van Ballenberghe 1972; Mech 1972, 1973). Individuals within a pack utilize a common territory or "defended area" (Noble 1939), and the home range of individual wolves, defined as the area in which they travel during normal activities (Burt 1943), coincides with the territory of the pack to which they belong. The Minnesota studies revealed

that packs usually occupy exclusive, nonoverlapping territories, with territory size and wolf density probably related to food supply.

In northern Minnesota wolves began to travel outside their former territory in response to a shortage of their principal prey, white-tailed deer, indicating that territories may be enlarged in response to a decreased food supply (Mech, in press). Along the Minnesota shoreline of Lake Superior, where deer densities are very high, wolf densities reached 1/14 km^2, with pack territories among the smallest reported for wolves (Van Ballenberghe 1972). Five resident packs totaling 40 wolves occupied an area the size of Isle Royale.

The inherent flexibility of territory size, demonstrated by these Minnesota studies, allows for great adaptability to local conditions. We would expect that a pack's territory would be no larger than necessary to obtain sufficient prey. A shrinkage of territory in response to an expanded food base allows for the establishment of additional packs, as on Isle Royale. Significantly, during the winter prior to the appearance of the East Pack on Isle Royale, the West Pack utilized only half of the island. Simultaneously, the amount of food available to Isle Royale wolves was higher than at any other time during this study (Table 10).

In 1972-74 Isle Royale had two primary packs, each occupying about half of the island. Additional duos and trios usually occupied areas along the boundary between the two large territories. Loners followed the large packs and scavenged their kills, or existed independently. As pack sizes increased from 1972 to 1974, the amount of spatial overlap between the two packs increased; there was a simultaneous decline in the calculated amount of prey available to wolves in both packs.

EXCLUSIVE TERRITORIES

Pack territories probably are no larger than the minimum size necessary to provide sufficient food and are sensitive to changes in density of vulnerable prey. This flexibility in territory size is advantageous to wolves in maximizing their hunting efficiency. Restriction of pack activity to a certain area ensures an intimate knowledge of that area (prey location and easiest travel routes) and prevents wasteful overlap in hunting efforts of two packs. A mechanism that spaces packs in relation to prey may be of greatest importance during the pup-rearing season, when pack activity is centered around the relatively immobile pups. Litters distributed so that there is plenty of food in the surrounding area would provide for rapid growth of pups.

The advantages accruing from a system of exclusive territories should apply equally well to other species of group-hunting carnivores. Indeed, the spotted hyena (*Crocuta crocuta*) exhibits a similar pattern of social organization and spacing, at least at high population densities (Kruuk 1972). At lower predator densities the "need" for exclusive territories would be lessened; Kruuk (1972) found that in the Serengeti, where prey are highly mobile in response to environ-

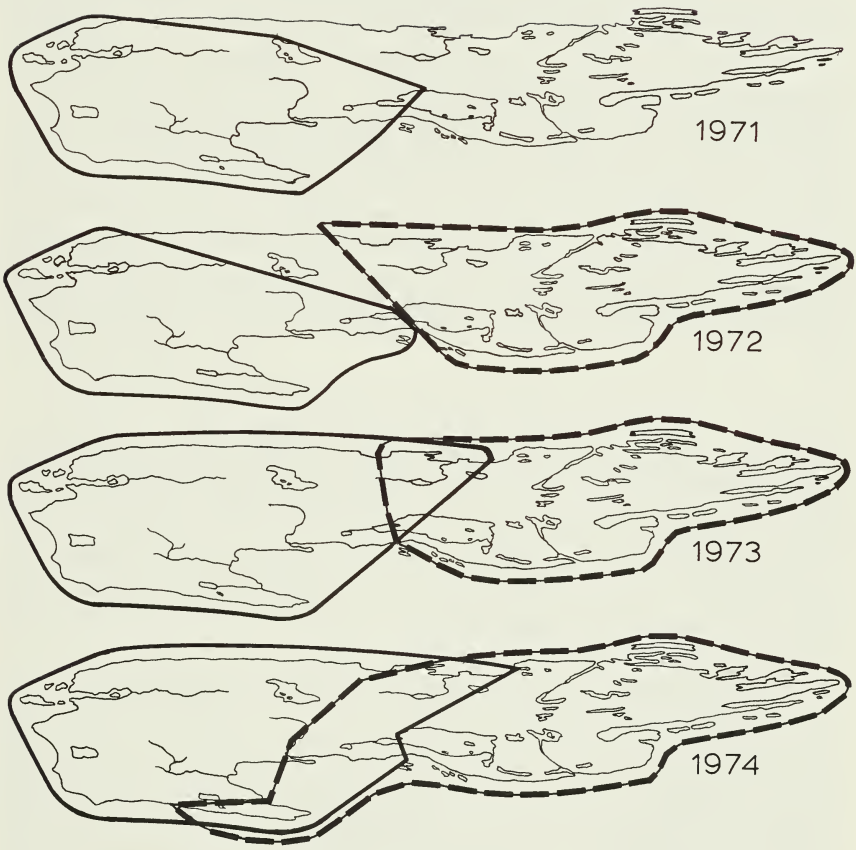


Fig. 58. Winter territories of Isle Royale wolf packs, 1971-74.

mental factors, the hyena population was relatively low and territories were not as clearly defined as in regions of higher hyena densities. Eaton (1974) suggested that naturally low densities of cheetahs might explain the lack of exclusive territories in this species.

TERRITORY SIZE

Territory size of the East Pack increased from 1972 to 1974, while there was no consistent trend in the range of the West Pack (Fig. 58; Tables 12, 13). Simultaneous with an increase in the territory of the East Pack there was a consistent decline in availability of food per wolf in both packs.

The amount of overlap in pack territories increased from 1972 to 1974. In 1972, the first winter for the East Pack, approximately 9% of the island was not utilized by either main pack. The following year the two packs overlapped on 6% of the island during winter. In 1974, the amount of overlap increased to 16% of the island, primarily because of the movements of the East Pack into traditional West Pack territory. It seems reasonable that the increased amount of overlap resulted from the growth of the East Pack, with a concurrent increase in the food requirement.

EXPANSION OF EAST PACK TERRITORY

When the East Pack moved into what had been regarded as West Pack territory in 1974 its behavior and movements were of great interest (Fig. 59). The following account was edited from field notes:

> Prior to February 1974, the East Pack had never been observed west of Siskiwit Lake. On 12 February, however, tracks indicated that it had traveled to Mud Lake, 2 km southwest of Siskiwit Lake. On 15 February we circled the pack as it crossed its former territorial boundary and entered Siskiwit Bay.
>
> As the pack approached Little Siskiwit Island the alpha female squatted and marked the ice with urine. Another wolf rolled on a spot at the tip of the island after sniffing the urine: a second rubbed its neck on the same spot. A subordinate wolf urine-marked the same place, and soon all the wolves clustered about the area with their noses to the ice. The alpha male marked once, and the alpha female marked again before they left the island. Frequent scent-marking was observed after they left the island (10 urine marks in 0.50 hour). Several subordinate wolves marked in addition to the alpha wolves. Urination posture for all wolves was either stretching forward or squatting; no raised-leg urination was observed. As they proceeded, the subordinate wolves usually clustered about the alpha pair in a mobile group ceremony.
>
> The alpha pair and two other wolves of the West Pack were resting by a kill on Francis Point, only 5 km away, across the frozen bay. Although ravens feedings on this kill saw the approaching East Pack and flew out to meet them, rough ice apparently blocked the view of the wolves.
>
> Fifteen minutes after the pack left Little Siskiwit Island, we left to refuel. On our return in 0.50 hour the East Pack was lying on the ice in the middle of Siskiwit Bay. Bad weather

allowed only 5 more minutes of observation—during this time the pack got up and began moving toward Houghton Point.

February 16: The East Pack wolves killed a moose when they reached Houghton Point and were resting on the ice at the end of the peninsula. Five West Pack wolves were at their kill only 4 km away.

February 17: Tracks showed that the East Pack traveled due west into Siskiwit Bay for about 2 km and then returned to its kill on Houghton Point. The tracks of the West Pack went round the head of Siskiwit Bay and then southeast until they met the tracks of the East Pack. The tracks then abruptly changed direction and crossed to the opposite side of the island.

February 18: Bad weather prevented any flights.

February 19: In the morning we found the East Pack lying on shelf ice on the south side of Houghton Point, about 1.5 km from the carcass of a wolf that it evidently had killed (Fig. 60). From tracks it appeared that there may have been as many as three wolves in the group that met the East Pack coming from Houghton Point. The dead wolf, a female pup, was definitely not a member of the East Pack (which was unaltered in size); we could only surmise that it was a member of the fragmented West Pack. The wolf had been deeply wounded in the throat area, and puncture wounds were frequent, especially in the rump region. None of the carcass had been consumed by the East Pack. The rump of the dead wolf had been heavily marked with urine, and three other fresh scent marks were found in the vicinity of the carcass.

Several hours later the pack resumed travel southwest along the shore. Scent-marking was frequent—at least four wolves urine-marked in 14 minutes (alpha female, two subordinates, and one of unknown status marked in either squat or stretch position). At the mouth of a small creek it encountered a well-used travel route of the West Pack. Most wolves had their noses to the ice. They quickly gathered around the base of a large spruce tree, crowding together in order to sniff its trunk, which undoubtedly had been previously marked by the West Pack (Fig. 61). Suddenly they scattered away in several directions, as if frightened. After standing briefly along the bank of ice next to shore, the alpha female led the pack back in the direction from which it had come, apparently in response to the first obvious sign of extensive West Pack activity that it encountered.

Several important aspects of the above account should be emphasized: (1) the East Pack, although it traveled into "foreign" territory, moved into an area that had not been used recently by the West Pack, and it turned back when it encountered significant West Pack activity; (2) the East Pack outnumbered any of the fragments of the West Pack with which it had direct or indirect contact. The alpha pair and two other wolves of the West Pack avoided areas crossed by the East Pack, even areas within their own territory; (3) as the East Pack ventured into areas probably unfamiliar to it, there was an unusual amount of scent-marking, by both dominant and subordinate members of the pack.

MAINTENANCE OF TERRITORY

Wolves must rely heavily upon indirect means of communication to delineate territorial boundaries. Potentially, any behavior which advertises the presence of a pack and causes another to avoid intrusion is of territorial significance. Scent-

TABLE 12. Numbers, movements, range, and prey availability for the West Pack, 1971–74.

Period of coverage		No. of wolves	Travel per day (km)	Pack range (km^2)	Area per wolf (km^2)	Prey available per wolf per day (kg)[a]	Average mileage between kills (km)[b]
1971	2 Feb.–9 Mar.	(8)–10	9.0	274.0	27.5	10.0	18.5
1972	27 Jan.–9 Mar.	8	9.5	246.4	30.8	7.4	39.8
1973	25 Jan.–26 Feb.	8	15.1	327.1	40.9	8.5	54.1
1974	21 Jan.–12 Mar.	12	not available	327.1	27.3	4.4	not available

[a]From Table 10.
[b]From Table 6.

TABLE 13. Numbers, movements, range, and prey availability for the East Pack, 1972–74.

Period of coverage		No. of wolves	Travel per day (km)	Pack range (km^2)	Area per wolf (km^2)	Prey available per wolf per day (kg)[a]	Average mileage between kills (km)[b]
1972	27 Jan.–9 Mar.	(8)–10	10.5	247.5	24.6	9.2	25.6
1973	25 Jan.–4 Mar.	13	13.5	252.4	19.4	6.2	42.8
1974	24 Jan.–10 Mar.	16	9.8	302.2	18.9	5.0	32.8

[a]From Table 10.
[b]From Table 6.

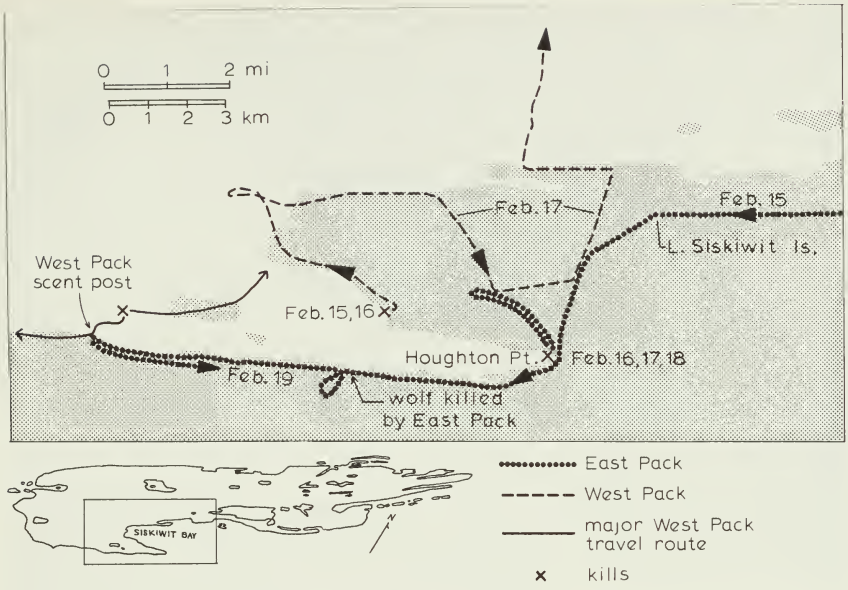


Fig. 59. Movements of the East Pack into traditional West Pack territory in 1974.

Fig. 60. Author recovering carcass of female pup killed by East Pack during trespass in 1974.

marking, howling, direct aggression, and avoidance may all serve to maintain territory.

Scent-marking. In addition to other functions discussed later, scent-marking serves to delineate territorial boundaries. The above account of the movement of the East Pack into West Pack territory is the only reported observation of a pack encountering another pack's scent-marks. One additional instance of avoidance behavior along a territorial boundary was deduced from tracks in February 1973 (Fig. 62).

Peters and Mech (1975) detailed four cases, determined from tracks, in which a pack responded to foreign scent-marks by avoidance. In one instance a pack chasing a wounded deer ceased pursuit at its territorial boundary. Generally, the outermost kilometer of a pack's territory was scent-marked profusely compared to the center. They concluded that scent-marking was an extremely important part of territorial behavior that contributed to efficient spacing among wolves.

Howling. Joslin (1967) suggested that howling may be of territorial significance, since it is an effective form of long-distance communication and may convey enough information to permit identification of howling wolves. Since the interface between packs on Isle Royale is so short and territories are long and narrow, howling may be a less effective method of communication between packs than it would be elsewhere.

Responses of wolves to human imitations of wolf howls are variable. In one case in June 1973, Sheldon L. Smith (pers. comm.) was sitting on a ridge less than a mile from where human imitations of wolf howls were being broadcast. Although he did not hear the human howls, he heard at the same time seven or eight brief howls from several wolves that were passing him through adjacent thick vegetation. The wolves seemed to be responding to the human howls, but were traveling in the opposite direction.

In another case, in September 1972, we elicited a howling response from several wolves in East Pack territory. We approached the group and howled again, and soon a single wolf approached us. Its body and tail markings suggested it was the alpha male of the East Pack. When the wolf saw us it turned and ran back to the rest of the group, and the pack disappeared. Only the one wolf, quite possibly the dominant male, left the others to confront what he might have thought were foreign wolves. Joslin (1967) was often approached by one or more wolves when he howled within 200 yards of homesites. He interpreted this as active resistance toward intruders.

Direct aggression and avoidance. When adjacent packs make visual contact with each other, such as across the ice of a large lake, they must either confront or avoid each other. The response of any two packs probably would depend on their previous history of association and perhaps their numerical strength. The East Pack killed a strange wolf even though it was in unfamiliar surroundings. The outcome of such a confrontation might well have been different if the East Pack had met the entire West Pack, instead of not more than three. Lack of numerical

a

b

Fig. 61. East Pack (a) gathered around West Pack scent post while trespassing in 1974, (b) standing on shore after scattering from scent post.

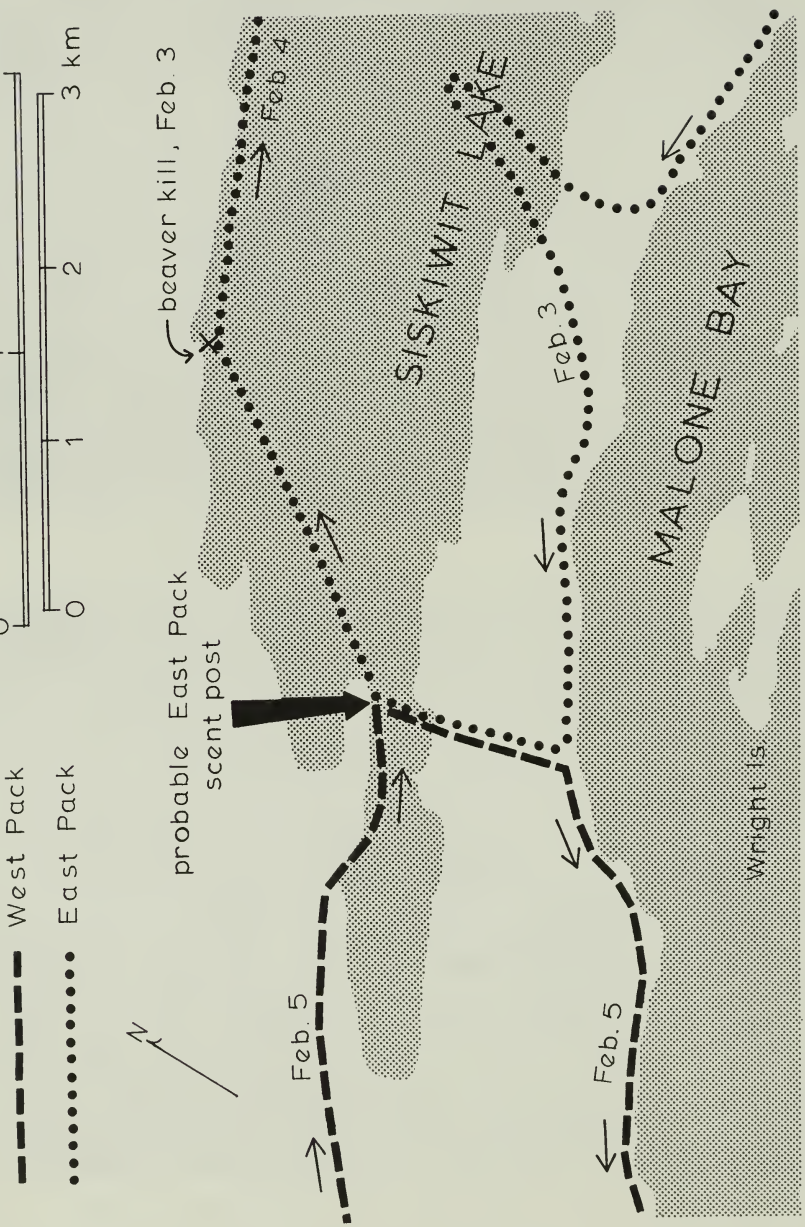


Fig. 62. Avoidance behavior of the West Pack in response to an East Pack scent post, 1973.

strength may have been the reason for the previously discussed avoidance of the East Pack by four West Pack wolves in Siskiwit Bay, even though the West Pack animals were in their own territory.

SMALL PACKS AND "LONERS"

In all 3 years that both East and West packs have existed, an additional, small group of wolves has been present (Fig. 63). In 1972, a pack of two or three was seen in the Malone Bay area, ranging over to Houghton Point and possibly as far as Chippewa Harbor. In the next two winters, two wolves (the "Todd duo") traveled the north shore in the vicinity of Todd Harbor and were also seen near Intermediate Lake and Lake Whittlesey. The smaller of the pair was noticeably reddish on its lower flanks and belly. Their friendly greetings suggested a male and female pair.

It is significant that in the years when two large packs "divided" the island approximately in half, the small pack usually inhabited an area either between the two packs or overlapped by each. This supports the hypothesis of Mech and Frenzel (1971:33), who believed that wolves in Minnesota were organized into breeding packs occupying exclusive territories, with "loners and other nonbreeding population units" inhabiting nonexclusive areas among the pack territories. These small groups probably survive only by their ability to avoid the large packs.

The "loners" are more difficult to locate and observe than the larger groups. Their ecology and social status relative to other wolves in the population is little known. Jordan et al. (1967) described several stages of "dissociation" of single wolves from a pack. They believed that many loners were aged and socially subordinate wolves that were gradually excluded from the pack, although in individual cases it is usually not possible to determine sex, age, or previous social relationships.

I have seen only one case in which a single wolf which was following a pack might have been a "dropout." After the West Pack declined from eight wolves to seven in mid-February 1972, a wolf was seen following it, often hesitating and apparently trying to remain hidden from the view of the pack. The pack had left the carcass of a moose near Windigo, traveled a short distance, and then lay down on the ice north of Beaver Island. The single wolf walked up on a 50-m rise on the north side of Beaver Island, then sat down at the edge of a cliff overlooking the pack and watched them intently, hidden from view by trees.

The different reactions of a pair of wolves to single wolves were recorded in 1974 (field notes):

> On February 6, 1 or 2 days after the West Pack fragmented, a pair of wolves (the McGinty Duo) were found on a kill at the southwestern end of the island. One wolf was larger than the other, and the friendly greetings suggested a male-female combination. On February 13 a single wolf, tracked from a previous kill of the West Pack, joined them. The single wolf participated in greetings between the duo, although it was very submissive. Perhaps all 3 were formerly included in the 12 wolves of the West Pack.

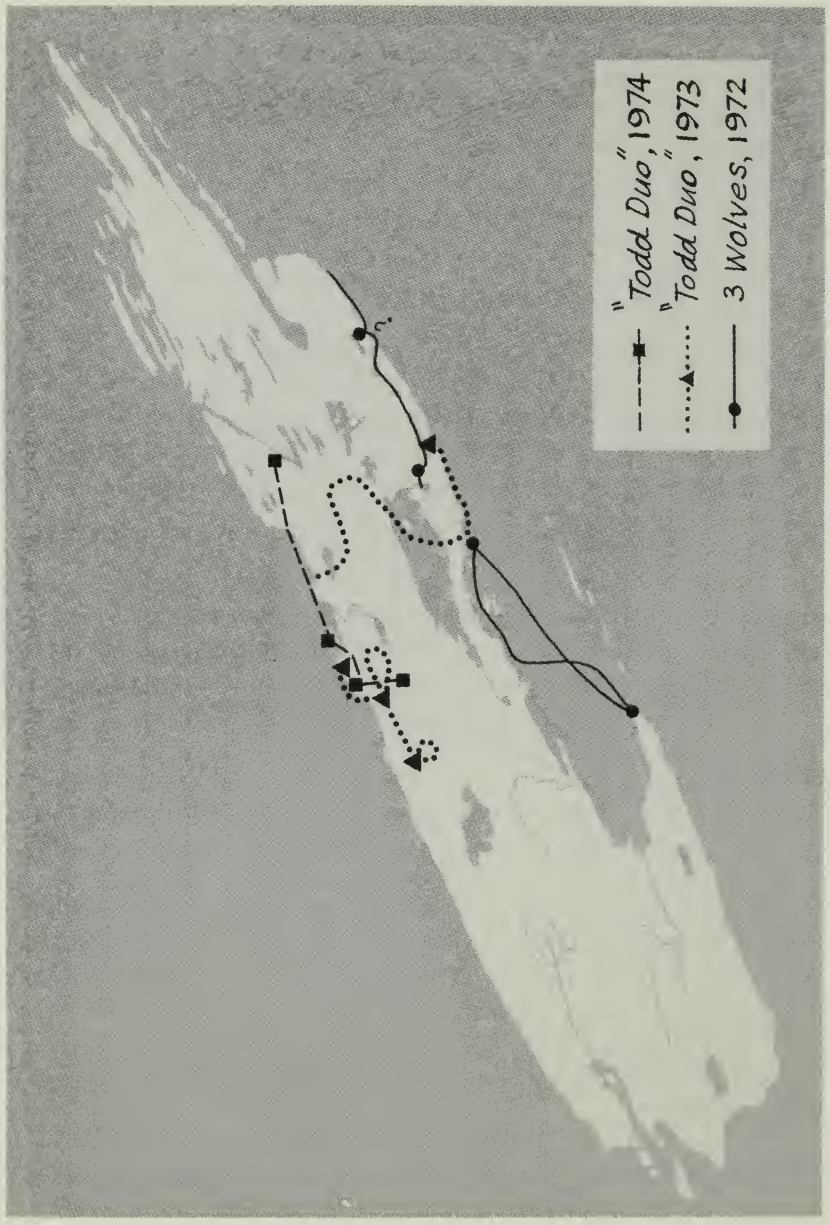


Fig. 63. Travel routes and carcasses utilized by small groups of wolves on Isle Royale in midwinter, 1972-74.

On February 14 we found another wolf following the tracks of the third wolf around the southwestern end of the island, and it appeared about to join the newly-formed trio, who were feeding on a kill on the ice at the entrance to Washington Harbor. However, when the fourth wolf was finally seen by the trio on the kill, the duo gave immediate chase, while the other newcomer stayed at the kill and fed. The duo chased the single down Washington Harbor at top speed, then followed it overland back to the lakeshore at the southwest end of the island. After running 5 km, the duo contined to follow the single for at least 19 km before returning to the Washington Harbor area, where they were again joined by the third member.

Communication Among Wolves

VOCALIZATION

The highly social nature of wolves and the flexibility of their group structure and hunting habits probably account for the diversity in forms of vocal communication found in this species. Howling, the most widely known and most unique wolf vocalization, is of obvious significance in long-range communication. Individual wolves have distinctly different howls and seem to be capable of distinguishing differences in howls, so there is a high potential for exchange of information via howling (Theberge and Falls 1967). Other widely recognized sounds that are not often heard in the wild include the whimper, growl, and bark (Mech 1970).

Howling. Howls can be heard for several miles under certain conditions, and Joslin (1967) reported that howling could advertise the presence of wolves over a 130–km^2 area. In addition to possible territorial significance, howling helps to assemble individuals in a pack after they have been separated. On Isle Royale in 1973, howling also was of obvious importance in coordinating moves of a large pack between summer homesites.

Spontaneous howling of East Pack wolves was heard 62 times during approximately 383 hours spent near their rendezvous sites (homesites) in 1973. Most of the howling was heard at night (Fig. 64), when more adults were hunting and spatially separate. Such howling may help wolves coordinate hunting efforts. Pups and adults at or near a homesite often howled in response to howls of distant adults. Almost half (45%) of the howls heard near East Pack homesites included adults that howled some distance away.

Increased howling at dawn and dusk may be associated with departures and arrivals of adults at the rendezvous areas. Carbyn (1974a) recorded dawn and dusk peaks in howling and general activity at wolf rendezvous sites in Jasper National Park in Alberta. Murie (1944) described how adults assembled at the den before departure for their nightly hunt. Howling at this time accompanied generally friendly behavior, with much greeting among the adults. Group howling and greeting ceremonies often occurred together among members of the captive pack at Brookfield Zoo (Fig. 65). Group howling also is common among coyotes and jackals (*Canis aureus*) (Kleiman 1967).

A group howl was observed at a summer rendezvous of the East Pack in July 1973 (paraphrased from field notes):

> In mid-morning the only wolves in view were four pups lying motionless in thick grass in a favorite resting place. An unseen adult in the woods nearby began to howl, probably in response to a distant howl that was faintly audible to us. Three unseen adults then began to howl at the rendezvous. Another adult wolf about 1 km from the rendezvous also joined the howl. The four pups became excited and chimed in with yips and short, high-pitched howls. One stood and howled with its head slightly raised, while the other three sat and howled with their muzzles pointing at the sky. The howling lasted for about 2 minutes, after which the pups looked briefly in the direction of the howling adults and then resumed their normal activities of playing, snapping at insects, and resting. Ten minutes later all the pups ran out the west side of the rendezvous and greeted an incoming adult.

Although wolves are capable of fine auditory discrimination, they may howl in response to sounds which, to human ears, are quite distinct from actual wolf howls. At Brookfield Zoo, howling often occurs in response to sirens. Human "howling" is often an adequate substitute for prerecorded wolf howls when attempting to stimulate howling among wolves. The common loon (*Gavia immer*) has a call that closely resembles a wolf howl—twice in 1973 Isle Royale wolves at summer homesites began to howl immediately after hearing loons. Once, the pups were clearly the first to respond. On two occasions I heard loons calling shortly after wolves began to howl.

Other vocalization. Only limited information was gathered on Isle Royale on other forms of vocal communication, mainly because they are inaudible at long distances. An adult whimpered when it arrived at a summer rendezvous after the rest of the pack had left. Whimpering, interspersed with occasional high-pitched yipping, was frequently heard from pups as they mobbed adults arriving at rendezvous sites. Joslin (1966) believed that whimpering was a friendly greeting, sometimes conveying a submissive attitude. Whimpering was often part of low-intensity, friendly greetings at Brookfield Zoo, especially between pairs during the mating season.

Barking was heard only during group howls at rendezvous areas. Much of the pup vocalization during group howls consisted of high-pitched "yips," and adult barking sometimes accompanied these pup vocalizations, especially near the end of a howl, much as Joslin (1966) described. He considered barking to be either of a threatening or alarm nature. The "alarm bark" is short and often seemed to cut off a howling session. Joslin occasionally elicited a threatening bark by howling at close proximity to wolves at a rendezvous. In such cases, the barking was more continuous and interspersed with growling.

SCENT-MARKING

Humans, with a poor sense of smell, are ill-equipped to appreciate the importance of olfactory communication. Scent-marking helps maintain territories, con-

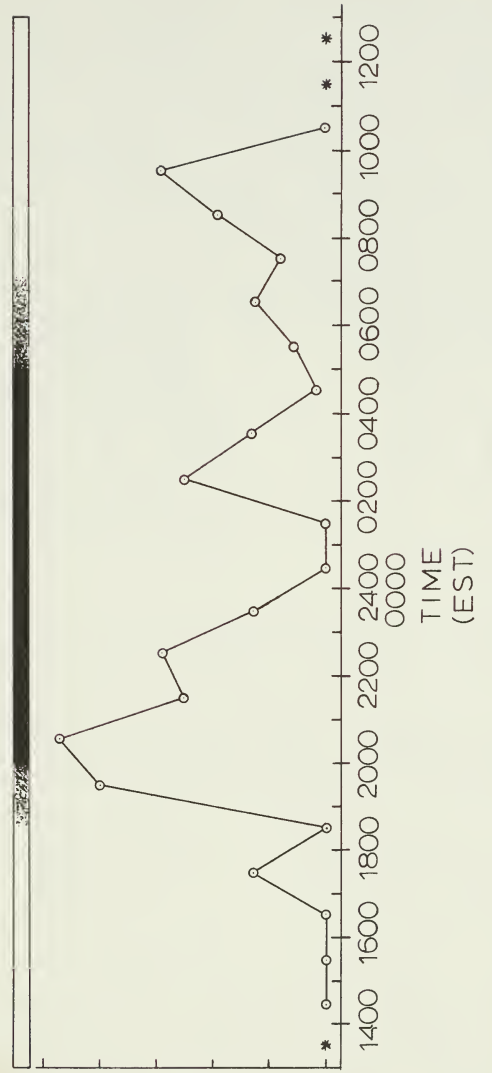


Fig. 64. Frequency of howling near East Pack rendezvous sites in 1973 (4 July-6 October).

Fig. 65. Group howl (Brookfield Zoo).

tributes to pair-bond formation, provides information on social and sexual status and individual identity, and helps orient wolves in their environment (cf. Peters and Mech 1975).

In canids, elimination (urination, defecation) and rubbing of certain body areas may have scent-marking significance (Kleiman 1966). Scent-marking differs from simple elimination by its directional and repetitive nature—that is, the same object may repeatedly be scent-marked. Kleiman also suggested that this form of scent-marking developed from autonomic responses to strange or frightening situations. Initially, scent-marking could have reassured an animal entering a strange environment and may have since acquired additional signal value in territoriality and courtship (Fig. 66).

Wolves have at least two specialized scent glands (Mech 1970; Fox 1971). The anal gland is located on each side of the anal sphincter; presumably scent deposition takes place with each passage of feces. A tail (precaudal) gland of unknown marking function occurs on the dorsal surface of the tail near the base, under a dark patch of hair (''dorsal spot'').

Urine is also of considerable scent-marking importance among wolves. In a field study based on tracking wolves in snow, Peters and Mech (1975) distinguished four types of scent-marks: (1) raised leg urination (RLU); (2) squat urination (SQU); (3) defecation (scats); and (4) scratching. They found that the RLU was the most frequent and significant type of scent-mark.

Scent-marking by Isle Royale wolves was observed only in winter, usually from the air. Scent-marking was often difficult to distinguish from normal elimination,

which seemed to be most common when packs were resting near kills or just beginning to travel. In these cases I ignored defecation and urination unless clearly directed at an object.

Frequency of scent-marking. Obvious differences in frequency of scent-marking occurred among Isle Royale wolves (Table 14). In all cases the packs were traveling. When the East Pack first entered "foreign" territory we observed 10 scent-marks in a half-hour of observations, compared to 2 in an equivalent length of time as the same pack reentered its own territory several days later.

The highest level of scent-marking occurred when three wolves (McGinty duo + 1) left a kill in full view of four wolves of the West Pack (including the alpha pair) who had bedded down 1 km away after following the tracks of the three for many miles. The West Pack wolves were not watching the trio, one of which glanced in the direction of the sleeping wolves twice as we circled. This wolf made six of the seven scent-marks observed. In this case frequent urinations might have resulted from autonomic responses to fear or apprehension and might not have been actual scent-marking.

Peters and Mech (1975) found that when packs traveled within a kilometer of the edge of their territories, the frequency of RLU's was twice as high as when packs traveled in the center of their territories. Thus, an accumulation of marks characterized territorial boundaries. The strongest stimulus to scent-mark was the mark of a neighboring pack. In one case when a pack discovered fresh tracks of a neighboring pack on its territorial boundary, these researchers found 30 RLU's, 10 scratches, 2 SQU's, and 1 scat. During normal travel in winter, wolf packs left a sign every 240 m on the average, including a RLU every 450 m. At their normal rate of travel of about 8 km/hr (Mech 1966), that implies an olfactory mark about every 2 minutes, with a RLU every 3 minutes. Isle Royale wolves demonstrated comparable marking frequency (Table 14).

Indicator of sexual and social status. The alpha male and female in all packs observed from 1972 through 1974 accounted for most of the recorded instances of scent-marking (27 of 39 cases). In all cases there was active courtship between the alpha wolves; scent-marking clearly played a role in these activities at times. On four occasions the alpha female was seen urine-marking an object, and the alpha male, usually right behind her, sniffed the location and then urinated on it. Twice the alpha female marked a scent-post of the alpha male. In these cases, scent-marking should be considered part of the mechanism of pair-bond formation, as Schenkel (1947) suggested. Twice an alpha male mounted the alpha female immediately after inspecting her fresh urine-mark.

The frequency of genital inspection of females during the mating season indicates the importance of olfactory cues in sexual behavior. Experimental work with domestic dogs reviewed by Johnson (1973) documented that urine from estrous females was more attractive to males than that of anestrous females and stimulated mounting among males. Peters and Mech (1975) found that the frequency of RLU and SQU increased before and during the wolf breeding season. During the

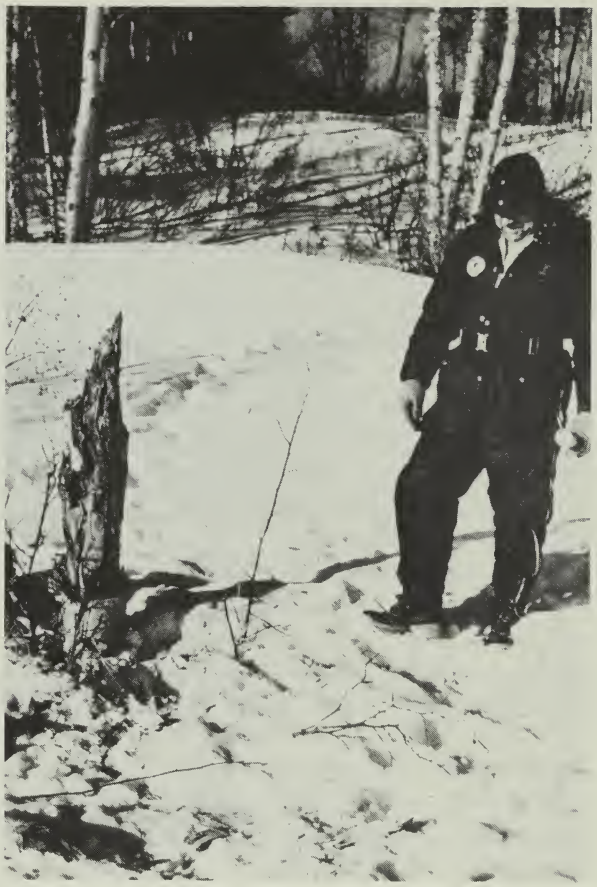


Fig. 66. Pilot D. Murray examines wolf scent post.

breeding season they often found a SQU and RLU together in the snow, indicating a female-male combination as described above.

We might surmise that scent-marking in the wild would be an important means of establishing initial contact between potential mates in widely dispersed populations. Peters and Mech (1975) pointed out that a lone wolf would be able to determine where potential mates lived and whether they were already paired off, since mating pairs often mark the same points. Also, territorial boundaries were marked with such clarity and frequency that a newly formed pair could easily tell whether they were in an occupied territory, along a territorial boundary, or in unoccupied space.

Limited data suggests that scent-marking is related to social status. Alpha wolves often marked when exhibiting no sexual behavior. In some cases subordinate wolves did not mark when they might have been expected to do so. For

TABLE 14. Scent-marking frequency in traveling wolves.

Date	Pack	No. of wolves	No. of scent-marks (urine or feces)	Minutes of observation	No. of minutes per scent-marks	Remarks
14 Feb. 1974	East	16	10	32	3.2	Pack leaving territory and crossing Siskiwit Bay.
19 Feb. 1974	East	14	4	14	3.5	Pack traveling in unfamiliar area and encountering foreign scent-post.
20 Feb. 1974	East	15	2	34	17.0	Pack re-entering own territory.
20 Feb. 1974	McGinty duo + 1	3	7	11	1.6	Pack leaving kill, with West Pack in view.

Fig. 67. Scent post and scratch mark of alpha pair, West Pack, 1972.

example, in 1972 the alpha female in the East Pack squatted and urinated on a ridge of ice as the pack was traveling. The spot was inspected by a subordinate wolf, who continued on its way without marking. The alpha male, however, lifted his leg and urinated on the spot after sniffing it. In 1973, four subordinate wolves of the West Pack followed the alpha pair into the woods next to shore. The alpha male led the way, marking a tree on the shoreline. The alpha female followed suit, but the other four wolves sniffed the scent post and left without adding their own scent. Mech and Frenzel (1971) recorded an instance when a wolf believed to be the alpha male was more active than the others when the pack encountered scent posts.

Peters and Mech (1975) reported that in two captive packs only high-ranking wolves raised their legs when urine-marking. Twice when they tracked wild pups, they found several SQU's, but no RLU's. While males tend to lift their legs more

often than females when scent-marking (Kleiman 1966), several alpha females did this on Isle Royale. I did not observe subordinate wolves lift a hind leg while scent-marking, at least while alpha wolves were present.

Orientation and information exchange. Scent-marking in canids may also serve for orientation and information exchange. Humans naturally regard visual signals as the most important means of orientation but, for wolves, a keen sense of smell would be more valuable. Scent-marks are frequent along pack travel-routes and are especially prominent around kills or other centers of activity. About half of the scent-marks recorded by Peters and Mech (1975) were at trail junctions.

Peters (1973) found that fatty acid content of anal gland secretions differed between males and females and that all individuals differed slightly from one another. Peters and Mech (1975) showed that wolves tend to remark fresh scent-marks more often than old marks, and inferred that wolves also could discriminate between marks of different ages. Thus, by simply sniffing a scent-mark, a wolf can probably tell whether the marking wolf was a stranger, a male or female and its reproductive status, and how long ago the mark was made.

Territorial marking. Young (1944) reported that wolves became greatly excited and scent-marked frequently when encountering the introduced scent of a strange wolf. Schenkel (1947) believed that scent-marking was of territorial significance; avoidance behavior in response to another pack's scent posts along a territorial boundary occasionally has been documented (see Maintenance of Territory).

Rolling and scratching. Kleiman (1966) believes that rolling has some scent-marking function (perhaps self-marking); Fox (1971) suggested that this may promote interaction with other pack members by encouraging social investigation of wolves carrying interesting odors. Wolves that are separated from the pack could transport odors on their fur and perhaps transmit information to other pack members. I have seen Isle Royale wolves roll at various places: a moose bed in the snow, the kill site of a fox, the dug-out remains of an adult moose killed 7 months earlier, and in snow next to a fresh moose kill. Also, when the East Pack reached Little Siskiwit Island on its trek into new territory, two wolves rolled on the ice after sniffing it; perhaps this was an old scent post.

Wolves often scratch with their feet after urinating and defecating (Fig. 67). Usually, only high-ranking wolves exhibit such marking (Peters and Mech 1975). The function of this behavior is not clear, but Mech (1970) noted that it would increase the visual signal value of a scent-mark. Schenkel (1947) thought that it might be a behavioral rudiment which perhaps has lost its original function. This is reasonable in light of comparative work with other carnivores. Kruuk (1972) found that male hyenas scrape only as a sexual display in courtship—probably to distribute the scent of their interdigital glands. While interdigital glands have not been described in wolves and coyotes, Fox (1971) stated that such glands are found in red foxes and perhaps existed in primitive canids.

Fig. 68. Rare look at wolves in summer. Second wolf running through brush in upper right.

Fig. 69. Wolves dug out this old den site (a beaver lodge) in March.

Summer Ecology

The shy and elusive nature of wild wolves makes summer ecological studies difficult. Significant observations in the wild are possible at dens or other centers of activity on the tundra of Alaska and Canada, but in forested areas rarely more than a fleeting glimpse of wolves is possible from the ground (Fig. 68). Radio-tracking has provided detailed knowledge of wolf movements in summer in Ontario and Minnesota (Kolenosky and Johnston 1967; Van Ballenberghe 1972; Mech and Frenzel 1971).

During this study, a den used by the East Pack was found in early July 1973. The wolves had abandoned it but were located at a rendezvous area 1 km away. Subsequent movements of the pack were followed to three additional rendezvous sites until pack movements became extensive in late September. One rendezvous site of the West Pack was found in September, about a month after it had been vacated. Direct observations of wolves were possible only at one rendezvous of the East Pack in 1973.

Dens

Wolves occasionally dig out dens weeks in advance of the birth of pups, which probably takes place in late April on Isle Royale. While wolves usually dig underground dens in sandy soil, they have also used hollow logs, rock cavities, old fox dens, and beaver lodges (Mech 1970). Dens commonly are close to water, perhaps because nursing females have a high water requirement.

The whelping den used by the East Pack in 1973 was an abandoned beaver lodge, whose entrance had been exposed when a dam broke. Another abandoned lodge 10 m away and a nearby hole in a sandy bank also appeared to have been used (Fig. 69). All holes were within 20 m of water. Many old scats under leaves and other debris indicated that this den had been used before—possibly during the first 3 years of the East Pack's existence. Tracks of a wolf were followed to this den in March 1974, and some scratching was found, but the site was not used in 1974.

Both lodges had a central chamber; barely large enough for an adult wolf, and many interconnecting tunnels which only pups could use. The only obvious alteration by wolves was the enlargement of at least one entrance and tunnel to the central chamber. Scattered around the den area were bones from at least six beaver, one muskrat, and one adult and one calf moose.

In 1975, the East Pack again denned in a beaver lodge. The West Pack denned in a hollow white pine (*Pinus strobus*) trunk that had fallen to the ground (Fig. 70). The log was 9 m long with the major opening 45 cm high and 55 cm wide. Pups frequently had used smaller openings created by decay of the wood. Three other possible whelping dens also were found—two abandoned beaver lodges and a hollow log.

Wolves visited all six dens during both summer and winter. Because there are very few opportunities for wolves to dig dens on Isle Royale, they take full advantage of existing structures.

Rendezvous Areas

In temperate regions pups are usually moved from the den site in late June or early July, after the pups have been weaned (Mech 1970). Thereafter, the activities of the pack center around "rendezvous sites" (Murie 1944:40) or "loafing areas" (Young 1944:103), where the pups remain while the adults make hunting forays. A succession of rendezvous sites are used by a pack until the pups are able to accompany the adults on all their travels.

Rendezvous sites, like whelping dens, usually are near water and often are adjacent to bogs (Joslin 1967). In 1973, five rendezvous sites were found on Isle Royale, four of the East Pack and one of the West Pack (Fig. 71). All five were located by abandoned beaver ponds, with water still available nearby. Size varied from 0.4 ha to a drainage 1 km long. Most had a prominent open area where the vegetation had been matted, and holes often had been dug in nearby banks. A small den was found beneath the roots of a cedar tree at one area, and a beaver lodge had been excavated and used at another area. Both dens and rendezvous are frequently reused, with former rendezvous sites possibly serving as den sites at a later date, and vice versa. Over a 3-year period, a pack studied by Carbyn (1974a) used the same den and the same first rendezvous site each year.

Rendezvous sites generally are used for shorter periods than den sites. Joslin (1967) found that packs moved an average of every 17 days, possibly influenced by frequent human howling nearby. Baffin Island packs moved to different summer dens (analogous to rendezvous sites) about every 30 days (Clark 1971); (Van Ballenberghe 1972). On Isle Royale, rendezvous areas were occupied from 11 to at least 48 days (Table 15). Wolves have been seen at rendezvous sites as late as October on Isle Royale and in northeastern Minnesota.

OBSERVATIONS AT A MIDSUMMER RENDEZVOUS

In July 1973, we observed the East Pack at its second rendezvous site from about 200 m. The pups usually were the only wolves in sight. Adults spent much of the day in the cooler forest surrounding a central open area. Most activity was observed before 11:00 a.m. or after 5:00 p.m.

Seven pups, probably the total in the pack, were seen at this rendezvous, along with at least seven different adults. Most of the adults in the pack probably visited the rendezvous periodically.

Adults were observed arriving at the rendezvous nine times, always before 10:00 a.m. or after 5:00 p.m. Only once did two wolves enter together, indicating

Fig. 70. West Pack den in hollow log.

Fig. 71. Aerial view of wolves at rendezvous site in October.

that most of the hunting effort by adults in summer is done by individuals or small groups. Pups often sensed the imminent arrival of adults and ran out as a group to meet them. Such an arrival was an occasion of great excitement for the pups, and they greeted the adults by yipping and jumping at their heads. Excited licking of the mouth acts as a stimulus causing regurgitation of food for the pups. On three occasions the arriving adults regurgitated food for the pups immediately, while being greeted. The pups ate such regurgitated food within a minute. Adults rarely remained in open areas for any length of time. About 11 kg of food per day would be required to feed seven pups; (based on Kuyt 1972); providing this amount is undoubtedly a demanding task.

Pup activity alternated with long periods of sleep, but even then pups frequently looked up or stood and readjusted their position. Their ears were in constant motion because of insects, mostly mosquitoes. When resting, pups often sought each other's company, even flopping down directly on another sleeping pup. Rest was interrupted with jaw-wrestling, scruff-holding, and occasional nibbling of legs and tails of nearby pups.

Many of the pup activities were group-oriented, such as play-fighting and competition for bones or sticks—appropriately termed "trophies" by Crisler (1958). Pups probably did most of the digging found at rendezvous sites. Many items were chewed extensively—moose bones, antlers (especially those in velvet), sticks, and at one site, an aluminum canteen. One evening, five pups gathered around a rotten birch log. They attacked the log in much the same way that they would later treat a moose carcass; each pup lay on its belly, chewing on its portion of the log and snapping at any encroaching sibling. They ripped enthusiastically at loose pieces of rotten wood and occasionally wandered off with a chunk for more peaceful chewing.

Six of the pups were of uniform appearance and impossible to tell apart. The seventh, called "7-up," was much lighter in color than the others. Its activities often set it apart. When first distinguished, this pup was the scapegoat during vigorous play-fighting of four pups. With tail firmly planted between its legs, "7-up" continually was the object of chases and alternately was submissive and

TABLE 15. Successive rendezvous areas of the East Pack, 1973.

No.	Dates wolves present	Minimum length of occupancy	Straight-line distance from previous rendezvous (km)
1	Mid-June (?)–21 July	19 days	–
2	19 July–29 July	11 days	1.0
3	ca. 27–28 July–23–24 Aug.	27 days	4.6
4	20 Aug.–6 Oct.	48 days	6.7

defensive. Another time, this pup was chewing on a calf-leg bone when two others walked up and stood over "7-up" with a dominant attitude; one finally grabbed the bone. After a spirited defense, "7-up" ended up on its back, entirely submissive.

On at least two occasions, "7-up" was the only pup at the rendezvous; once it appeared that no other wolves were present. During this time a cow moose walked slowly into the open area while the pup was out of sight. She stopped and sniffed the ground thoroughly. Undoubtedly, the scent of wolf pervaded the area, and she seemed hesitant, her movements very slow. Every few steps she stopped and looked about, frequently sniffing the ground in matted places. Finally she walked down the drainage and disappeared. Almost immediately, "7-up," with nose to the ground, scampered into the opening and followed the moose briefly. It is quite possible that the pup had had the moose under surveillance but was reluctant to show itself when the moose was nearby. Crisler (1958) and Fentress (1967) reported that their captive wolves were initially afraid of large animals, even traditional prey. Considerable experience is probably necessary before pups become effective predators of ungulates as large as moose. Moose commonly exhibit no fear of wolves. They were seen several times browsing on the edge of a rendezvous. Once I watched a bull, apparently unconcerned, browsing within 100 m of some pups and adults that were howling just out of sight.

MOVEMENTS BETWEEN RENDEZVOUS SITES

Wolves move to different rendezvous sites for seldom-known reasons. The accumulation of feces and debris eventually may render dens less desirable (Young 1944; Rutter and Pimlott 1968); perhaps the same applies to rendezvous sites. In some cases wolves might move the pups to a fresh kill. At two of the five rendezvous examined in 1973, a moose-kill was found in the center of the activity area (Fig. 72). At the rendezvous that the pack reused in 1974, a fresh kill was found in almost the same location as a kill that had been made the previous year.

We watched the East Pack abandon its second rendezvous of 1973. Howling helped to coordinate the move to a new site, as shown by the following field notes:

> Early in the afternoon of 28 July no wolves were visible, nor were any vocalizations heard until 5:00 p.m., when a single pup howled briefly, then whined. An hour later an adult howled, and in the next 2 hours howls of adults were heard seven times, although no wolves could be seen. Most of the howling was done by one wolf, although once, four adults howled simultaneously. No pups howled with the adults. At 9:30 p.m. an adult arrived at the rendezvous, and "7-up" ran out to greet it. The adult ignored the single pup, and as two adults howled in the adjacent woods this newcomer joined in, then trotted off toward them. The pup wandered about alone among the trampled vegetation, often with nose to the ground. The adult came back into the opening and played with "7-up" for several minutes but then left the pup alone again. At 10:00 p.m. the pup disappeared from view, and at 10:03 p.m. one pup and three to four adults howled together. A single adult howled briefly at 10:06 p.m. Observations ended at 10:10 p.m., and no more howling was heard that night. Although pups had often been absent in the past, the length

of the separation and the unusual amount of adult howling suggested that some of the adults and six of the pups had abandoned the area.

The next morning observations began at 6:40 a.m. At 7:15 a.m. the same adult walked into the rendezvous area again and stood still for a minute, sniffing the air. It whimpered loudly and sat down for another minute, constantly looking around and sniffing the air, then left. An hour later the alpha female arrived and was enthusiastically greeted by "7-up." She did not regurgitate for the pup, but walked the length of the activity area, sniffing the air and looking about. She disappeared, followed a short while later by the single pup. Between 1:00 and 2:00 p.m. howling of one or two adults was heard twice near the rendezvous. In the evening both the alpha male and alpha female arrived individually and lay down in the open activity area. "7-up" joined the pair, lying down near the alpha male.

Two hours later I heard a faint howl in the distance, and the alpha male rose and howled in response. The female joined him, as did another adult out of view. They howled continuously for 2 minutes, and after rubbing muzzles in a greeting, the alpha pair left the rendezvous, heading in the direction of the distant howls. Two minutes later the pup, who had remained silent throughout the howling, followed the pair. The rendezvous was silent for the rest of the night. The area was observed the next day to verify that the rendezvous had been abandoned.

Earlier in the summer, five pups were observed en route from the first to the second rendezvous. In this case adults were howling periodically at both locations, and the five pups went to the next site by themselves. The following day, a sixth pup was still present at the first site. Two nights after initial occupancy of the second rendezvous, adults present at the first site were heard howling in response to pups and adults at the new site, indicating that several days may be necessary for complete relocation.

Pup Production

Although pup mortality is widely regarded as an important factor controlling wolf populations, information on pup production and survival on Isle Royale is very limited (Table 16). Sometimes the minimum number of pups in packs can be estimated during winter, but this is not a valid year-to-year index.

Pup condition may provide some indication of the extent of mortality. A dead, emaciated pup was found in 1964 (Jordan et al. 1967), suggesting that inadequate food supply early in life might be a critical factor on Isle Royale. A decrease in food supply seems to be an important reason for poor pup condition and low survival in Minnesota (Mech 1973; Van Ballenberghe and Mech 1975; Seal et al. 1975). Kuyt's (1972) data suggested lower pup survival in areas where tundra wolves relied heavily on small mammals when caribou were absent.

A visual comparison of pups on Isle Royale and in Minnesota suggests that the pups on the island were faring well. I first saw the East Pack pups in late July. Subsequently I saw four pups, weighing between 8 and 13 kg, live-trapped in northern Minnesota in late September. By comparison, the Isle Royale pups seen 2 months earlier weighed about 9-12 kg. This is within the range of weight of captive

Fig. 72. Well-utilized carcass of adult moose killed by wolves in summer.

pups of the same age (Kuyt 1972), and is higher than weights of pups caught in Minnesota, where there was a food shortage (Van Ballenberghe and Mech 1975).

Two pups of the East Pack were seen about a month later. Growth in the intervening period was obvious; weight was estimated at 16 kg. They appeared full-bodied, with well-developed coat and guard hairs. These two pups were larger and appeared heavier than the four pups caught in Minnesota a full month later.

These observations of Isle Royale pups suggest that the midsummer food supply, at least in 1973, was sufficient for normal growth and development. However, there can be great differences in pup weights even within a single litter (Van Ballenberghe and Mech 1975). There was some evidence of retarded winter pelage development among some pups in the East Pack in February 1974 (Fig. 73). Nonetheless, winter observations of this pack since 1972 indicate rapid numerical growth, suggesting high pup survival from 1971 through 1973 (three successive litters).

Relations with Nonprey Species

In winter, wolves encounter scavengers for which moose carcasses are a principal source of food. Besides the red fox, many birds also utilize wolf-killed moose—primarily the raven, gray jay, black-capped chickadee, and an occasional eagle. Only the fox and raven will be considered here.

TABLE 16. Pup production on Isle Royale, 1970–73.

Natal year	Minimum no. of litters	No. pups present in summer	Minimum no. of pups present, following winter[a]
1970	1	unknown	2, West Pack
1971	2	unknown	probably 6, East Pack unknown, West Pack
1972	2	unknown	4, West Pack 3, East Pack
1973	2	unknown, West Pack 7, East Pack	4, West Pack 4, East Pack

[a]Interyear comparisons are not considered valid because of biases affecting winter identification of pups.

Red Fox

While wolves were seen chasing foxes six times in winter 1972-74, none was caught. Foxes can often run on light snow crusts where wolves break through, and they invariably outrun wolves when chased overland in snow. In the only chase seen on ice, the fox had such a long head start that it reached the shore with no trouble. In 1972, the East Pack was observed just leaving a fox it had killed on the open ice of Malone Bay. The area was matted with wolf tracks, and much hair had been pulled from the fox, though it was not eaten.

The fox's ability to outrun wolves in most snow conditions may be an important reason for its continued coexistence with wolves on Isle Royale. Coyotes, however, disappeared from the island around 1957, less than a decade after the arrival of the wolf. Foxes have thrived recently on Isle Royale, and perhaps even increased after the disappearance of coyotes. While foxes have been observed on Isle Royale since the mid-1920s, long-time island residents report that foxes were uncommon, at least relative to coyotes, before wolves became established.

Moreover, less competition for food resources exists between wolves and foxes than between wolves and coyotes. Johnson (1969) reported that snowshoe hares were the most important year-round food for Isle Royale foxes, and that at certain seasons they made extensive use of insects and fruit. Coyotes relied heavily on moose carcasses. Wolves apparently eliminated coyotes on Isle Royale (Mech 1966; Krefting 1969; Wolfe and Allen 1973), probably through direct killing and competition for food.

Fig. 73. Probable pup in East Pack, 1974. Note lack of characteristically stiff guard hairs.

Wolves occasionally were indifferent to the presence of foxes. In 1973, the West Pack bedded down on the ice after feeding on a moose carcass. Soon a fox approached, cautiously staying out of sight of the wolves when possible. At the carcass, the fox chased away several ravens and woke the wolves in the process, but they merely raised their heads for a brief look.

During winter periods when foxes were unable to catch snowshoe hares because of deep snow they relied heavily on carcasses of wolf-killed moose (Fig. 74). Foxes have difficulty penetrating the thick hide of a moose—they depend on wolves not only to kill the moose but also to open it up. In winters when utilization of kills by wolves is less than usual, moose carcasses may attract a large number of foxes—as many as 10 at one time in 1972 (Appendix G).

Raven

Ravens on Isle Royale in winter are almost entirely dependent on food indirectly provided by wolves (Fig. 75). Ravens often accompany the large packs in their travels, sitting in trees when the wolves stop to rest. Fresh kills draw ravens from miles—28 ravens were seen once on a moose carcass. Ravens also eat wolf scats, especially fresh ones with much incompletely digested meat. Similarly, they feed not only on fresh mountain ash fruit but also on fox scats that are loaded with fruit remains.

Fig. 74. Wolf kills provide food for scavengers such as red foxes.

Fig. 75. Ravens are found at virtually all wolf kills.

Since ravens and wolves often feed on the same carcasses, there is much interaction. Ravens seem to tease resting wolves, swooping low over their heads, landing nearby and hopping close, further arousing the wolves (Murie 1944; Crisler 1958; Mech 1966). Wolves, in turn, leap at ravens in the air, stalk them on the ground, and scatter them from kills.

In February 1974, Don Murray and I were circling a kill of the West Pack, with four wolves resting nearby. Suddenly a wolf made a couple of quick bounds—it had caught a raven, something Murray had not seen in 16 winters of flying on Isle Royale (Fig. 76). The wolf shook the raven vigorously in its mouth, then trotted by two other wolves, lay down on its belly and shook it again. Another wolf followed with great interest but was repulsed by a snap from the prize-holder. Finally, the wolf with the raven buried it in snow among some alders and trotted out to greet the other wolves. Next, it dug out the raven and paraded around with it in its mouth, always refusing to let the other wolves inspect it closely. After 15 minutes of this activity we left, but returned an hour later to find the wolves still playing with the raven's carcass. One wolf buried it below a shelf of ice next to shore, then stood above it while another wolf closed in on the buried trophy. When the wolf below came within 2 m, the one above leaped off the ledge and rolled the other over. A brief chase ensued, and then the whole pattern was repeated. The following day the wolves were gone, leaving the raven carcass in the snow.

Fig. 76. Wolves playing with carcass of raven they caught near a kill.

"COW AND CALF"

3
Moose Population Dynamics

An accurate portrayal of interactions between wolves and long-lived prey such as moose requires extended study. Sixteen years of accumulated information now allow some conclusions about fluctuations in moose numbers, productivity, and survival patterns.

Recent changes in vulnerability of moose to wolf predation, lowered calf production, and some evidence of malnutrition have emphasized the role of food supply in regulating moose numbers, contrary to the initial conclusions of Mech (1966). These changes reflect complex ecological relationships. Changes in habitat and other environmental variables—primarily snow conditions—have modified food availability and have underscored food supply as the ultimate factor determining numbers of moose on Isle Royale.

Although wolf predation does not control moose numbers in the usual sense (i.e., hold the population below the level where food supply had an effect), it is the primary mortality factor operating on this herd. Predation is the key factor shaping the adult survival pattern.

An Historical Perspective

The moose is a rather recent colonizer of Isle Royale (Fig. 77), probably swimming from nearby Ontario early in the present century, about the same time that moose populations on the mainland increased (Mech 1966). With no effective predators and an abundant food supply, the population grew to very high levels by the late 1920s. From ground observations, Murie (1934) estimated 1000-3000 moose present in 1929 and 1930. Browse depletion was evident at that time, and significant mortality from malnutrition apparently reduced the population to several hundred animals by the mid-1930s (Hickie 1936).

During the dry year of 1936, two large fires burned over 100 km^2 of Isle Royale. Aspen and birch regeneration in the burn provided a renewed food supply, and the population again grew until direct mortality from malnutrition was observed in the late 1940s (Aldous and Krefting 1946; Krefting 1951). In 1947, a population of 600 moose was estimated by aerial strip count (Krefting 1951).

Wolves became established on Isle Royale in the late 1940s (Mech 1966). Though wolves undoubtedly were killing moose soon after their arrival, the initial effect of their predation is unknown. By flying overlapping strips and buzzing moose to flush nearby animals, Cole (1957) counted 242 moose. He estimated the 1957 population at 300. Three years later, however, Mech (1966) saw 529 moose on a similar census. He estimated 600 moose, conservatively, and concluded that wolf predation was keeping the moose population within the limits of its food supply.

Recent Moose Numbers

In the years following Mech's study, other researchers refined moose inventory techniques; however, inherent biases and wide sample variances among moose population estimates remained a problem. Even so, the moose population apparently increased during the 1960s (Wolfe and Jordan unpubl. data) and leveled off or perhaps even declined from 1970 to 1974. Population trends from 1964 to 1970 are reviewed briefly and data from 1970 to 1974 are presented in detail.

Population Size, 1964-70

Estimates of the moose population made by aerial censuses (Table 17) suggest that moose increased from 1960 to 1969. Improved counting procedures and accumulated experience probably explain some of the increase. Mech's (1966) estimate of 600 moose in 1960 allowed for a 12% adjustment for moose that were missed, but probably no more than two-thirds of the moose could be seen in strip counts. Even if Mech's estimate for the 1960 population were adjusted accordingly, there is still enough disparity between the 1960 and 1969 counts to indicate an increase in the population in the intervening period.

Fig. 77. Young bull moose in summer.

Wolfe and Jordan (unpubl. data) consider moose pellet counts, 1964–70, to be a more accurate population index than the aerial censuses. They used the 1969 aerial census to "calibrate" the pellet counts, producing their "best estimate" (Table 17). They concluded that the population rose considerably between 1964 and 1967 and stabilized somewhat at around 1300–1600 moose from 1968 to 1970. Moose pellet counts made by Krefting (1974) also suggest an increasing moose population during the 1960s.

Use of pellet counts as population indicators assumes that defecation rates are constant throughout the study. Defecation rates may vary with quality and digestibility of food. Krefting's pellet counts rose steadily from 1950 to 1970; during the same period, the available browse supply declined. Increased use of less preferred, less digestible, browse species may have contributed substantially to the increased pellet counts.

Population Size, 1970-74

Midwinter aerial censuses in February 1972 and 1974, produced estimates of 818 ± 234 and 875 ± 260 moose respectively (Table 18). In 1972, zone boundaries were based mainly on the distribution pattern shown in Jordan et al. (1967). In 1974, the zones were redesigned with reference to current signs of moose, vegetation types, and elevation to reflect moose distribution more accurately. Four zones initially were assigned both years, but the results from the two lowest-density zones were similar and were combined as one in the table.

TABLE 17. Population estimates for the Isle Royale moose population, 1960–74.

Year	Observer	Estimate from aerial census ± 95% confidence interval	"Best estimate"[a]	Remarks (re: aerial census)
1960	Mech	600 –	–	Complete coverage, strip counts.
1964	Jordan	704 –	821	10% coverage, strip counts.
1965	Jordan	845 ± 300	897	Small, random plots, intensive circling.
1966	Jordan	705 ± 222	1274	Stratified sampling, intensive circling.
1967	Wolfe	531 ± 184	1614	Ditto 1966. Aerial estimate considered low.
1968	Wolfe	1015 ± 230	1279	Ditto 1966.
1969	Wolfe	1150 ± 266	1362	Ditto 1966. Considered Wolfe's "best" aerial count.
1970	Wolfe	945 ± 242	1449	Ditto 1966.
1972	Peterson	818 ± 234	–	Ditto 1966.
1974	Peterson	875 ± 260	–	Ditto 1966.

[a]Wolfe and Jordan (unpubl. data). Estimate based on annual variation in pellet group counts, calibrated according to Wolfe's 1969 aerial census reduced 5.3% to allow for late winter and spring mortality.

The irregular distribution of moose in midwinter is shown in Figs. 78 and 79. In 1974, the low density zone included most of the 1936 burn and much of the predominantly deciduous forests in the interior of the island, especially at higher elevations. Almost half of the island but only 15% of the population was included in this zone in 1974. Conversely, only 14% of the island but over half (57%) of the estimated population was included in the high density zone of shoreline and small islands, primarily areas of coniferous vegetation.

If an arbitrary 20% is added to the 1972 and 1974 estimates to account for moose that were missed, the resulting estimates would be 1023 and 1094 moose, respectively. These figures are lower than the 1969 estimate of 1438 (assuming an adjustment of 20%), but the differences are not statistically significant.

Relative mortality and reproduction, when compared to earlier conditions, indicate a probable decline since 1970. Judging from the number of kills found during annual winter studies since 1970, predation by wolves, especially on calves, has been consistently high (Appendix L). In addition, summer observations and fall aerial counts indicate low calf production and survival.

In spring 1974, it was still obvious that moose densities were high, relative to food supply. During 3 months of field work, six moose were found which appeared to have died of malnutrition. Even if the population has declined since 1970, heavy browsing in critical wintering areas during previous years could have long-term effects on forage production. Recent studies of browse production and utilization at the southwest end of the island indicate that moose densities in that area have remained high (Belovsky et al. 1973).

Moose population fluctuations in the near future will probably reflect a slowly contracting food supply unless fire intervenes. Winter conditions, which greatly modify food availability and energy requirements, will contribute to short-term variations.

Sex Ratio and Productivity

The proportion of adult males to females has a bearing on potential calf production (productivity), which is basic to an understanding of population dynamics. While the sex ratio of the Isle Royale moose herd is currently even and has apparently fluctuated little over the past two decades, calf production has shown a downward trend from 1959 through 1974. Net productivity (calves surviving their first year) seems to be relatively low, especially in those generations born after severe winters.

Sex Ratio

Aerial classification of 423 moose (365 adults) in October 1972-74 showed that the sex ratio of the Isle Royale moose herd was essentially even (Table 19).

Although such counts often were flown during the 1960s, changes in methods preclude use of these counts for sex ratio variations 1959-74.

The collection of skeletal remains of moose was used to check for significant long-term trends in the adult sex ratio. There was no apparent shift from an even sex ratio among adult moose dying from about 1950 to 1974 (Table 28). The slight majority of males in the total collection (54.5%) is not statistically significant (95% confidence interval is ±4.5%) and can be explained by the fact that male skulls with antlers are more easily found than skulls of females.

Other studies of naturally regulated moose populations have found that adult sex ratios are about even (Peek 1971a; Shubin and Yazan 1959; Knorre 1959). After reviewing North American and European studies, Bubenik (1972:276–295) concluded that in naturally regulated populations males occurred in equal proportion to females, with perhaps a slight excess of males in some areas.

Productivity

The percentage of calves in the moose population has been determined from aerial counts in fall and winter; summer field observations provide an index to the twinning rate (Fig. 80). These data can be used to estimate net productivity. The age at which cows first produce calves is unknown for Isle Royale moose, although

TABLE 18. Results of aerial moose censuses on Isle Royale, 1972 and 1974.

Zone	Area (km^2)	No. of plots	Proportion of zone counted	Moose counted	Moose per km^2 (s.d.)	Estimated total
			1972			
1	312.7	17	6.4%	5	0.25(0.12)	78
2	149.2	8	6.8%	19	1.87(0.52)	279
3	91.2	18	20.2%	93	5.05(0.87)	461
Whole island	553.1[a]	43	–	117	1.48	818±234[b]
			1974			
1	268.9	12	5.2%	7	0.50(0.26)	135
2	209.3	8	4.6%	11	1.14(0.32)	239
3	76.8	16	19.0%	95	6.52(1.10)	501
Whole island	555.0[a]	36	–	113	1.58	875±260[b]

[a]Slight discrepancies in island area arose from different methods of area determination. A planimeter was used in 1972; a dot grid (256 dots/in^2) was used in 1974.

[b]95% confidence interval for the population estimate, calculated according to the method of Wolfe and Jordan (unpubl. data). See Appendix H.

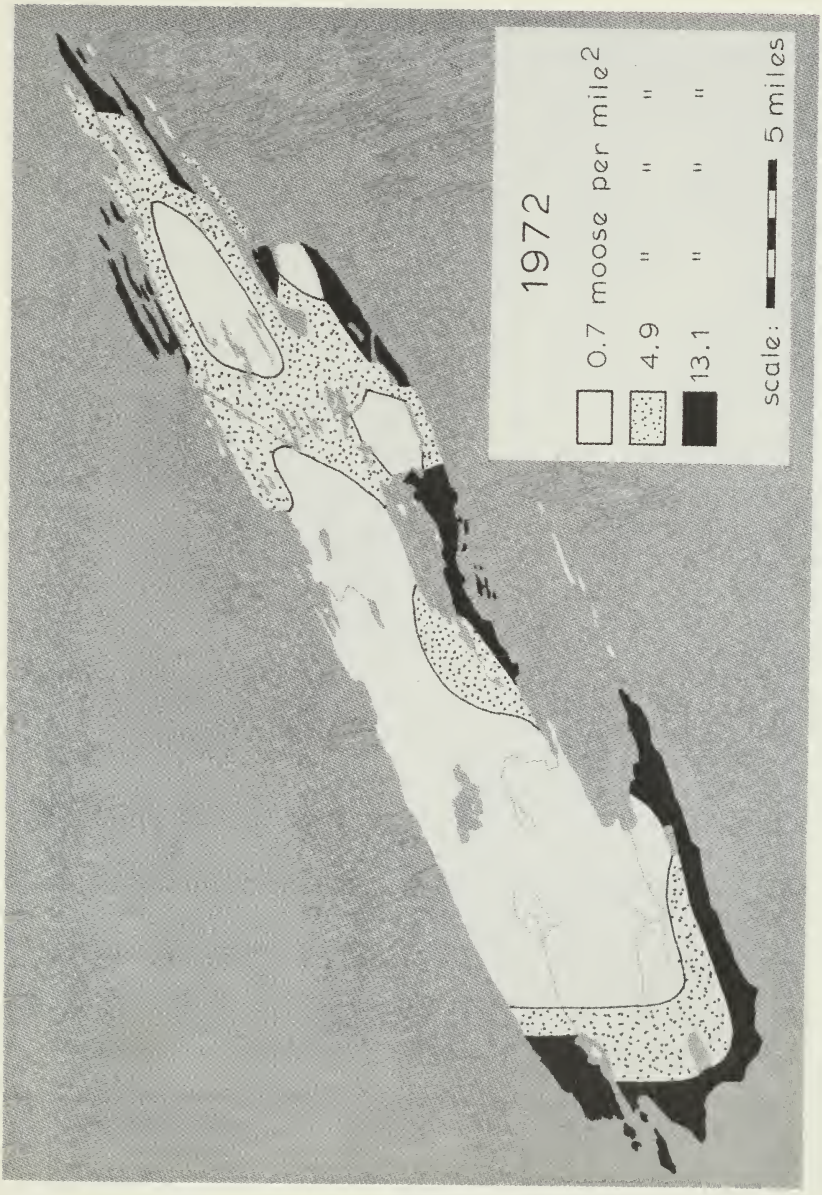


Fig. 78. Relative distribution of moose in February 1972.

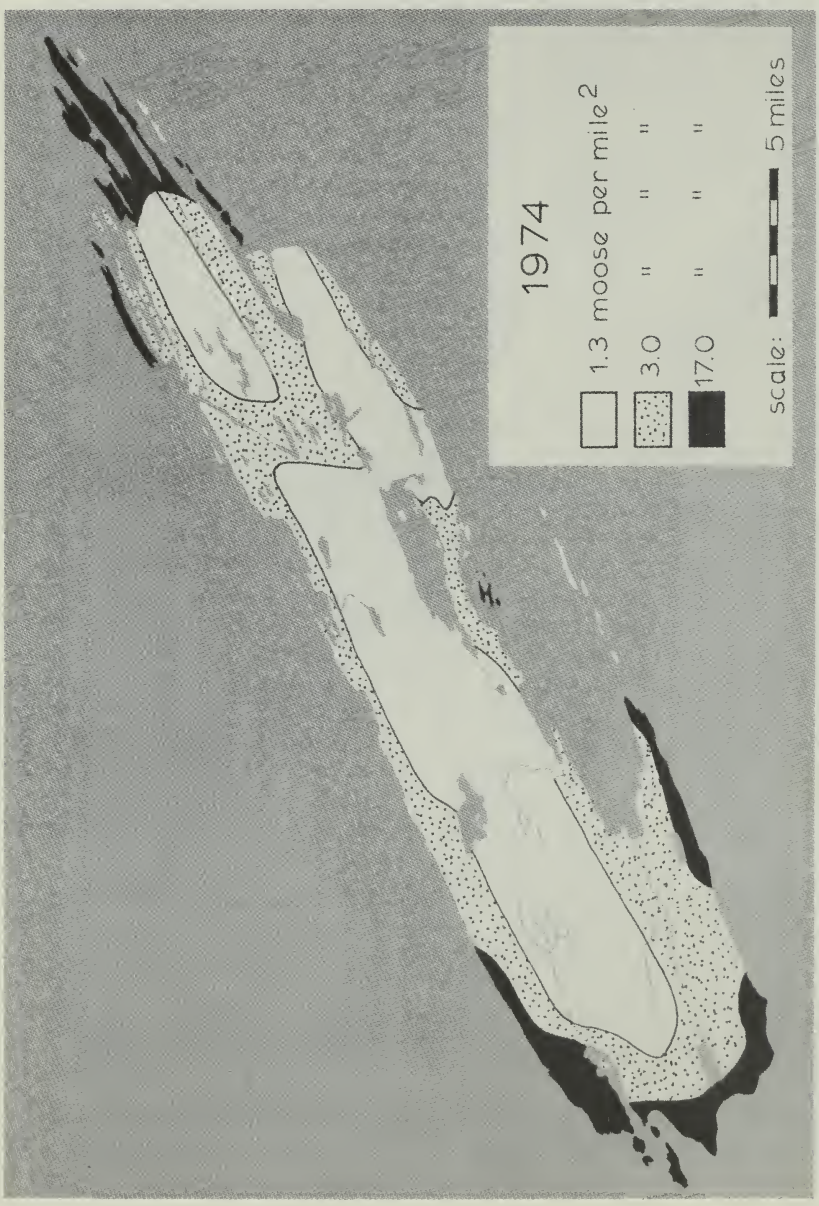


Fig. 79. Relative distribution of moose in February 1974.

TABLE 19. Fall aerial classification counts of Isle Royale moose, 1972–74.

Date	Total observed	Bulls[a]		Cows	Calves	Males/ 100 females	% calves[b]	% yearlings[c]
		Ad.	Yrl.					
17–19 Oct. 1972	114	47	2	53	12	92.5	10.2	4.1
23–25 Oct. 1973	192	73	8	81	30	100.0	15.6	9.9
22–25 Oct. 1974	117	43	7	51	16	98.0	13.6	14.0
Total		180♂♂		185♀♀				

[a]Bulls with spikes or small forked antlers were considered yearlings.
[b]Assuming an even sex ratio, % calves = no. calves/[2 (no. cows) + no. calves] × 100%.
[c]% yearlings = yearling bulls/(adult bulls + yearling bulls). This is analogous to "net productivity," as defined by Pimlott (1959).

Fig. 80. One-month-old moose calf.

other studies indicate that most females older than yearlings become pregnant each year (Pimlott 1959; Simkin 1965; Schladweiler and Stevens 1973). Changes in twinning rates best reveal long-term trends in productivity of Isle Royale moose.

CALF RATIOS, 1970-74

Moose herd composition, summer-fall in 1970-74, is shown in Table 20. Numbers of calves classified during fall aerial counts are probably more accurate than those made on the ground in summer. However, the fall aerial counts show a similar relationship to summer ground observations 1972–74, suggesting that the latter may provide at least a relative index to the calf segment.

Low calf numbers in summer 1971 and 1972, correspond to unusually deep snow the previous winters. Severe winter conditions probably were responsible for the low calf production. The relatively high calf crop in 1973 after a particularly mild winter further indicates that winter conditions may be important to productivity the following season. Ling (1970) correlated moose calf numbers with the severity of the preceding winter. He indicated that severe winters could affect calf production two summers hence by retarding the development of calves in their first winter and lowering their productivity as yearlings. Pimlott (1959) and Markgren (1969) believed that fertility of yearlings was quite dependent on nutrition during their first winter. Since yearlings comprise a relatively large segment of the adult population, a decline in fertility of female yearlings would greatly decrease

TABLE 20. Moose herd composition, summer and fall, 1970–74.

	Summer ground observations					Fall aerial counts		
	9 June–4 Sept. 1970	18 May–7 Sept. 1971	9 May–22 Sept. 1972	4 May–30 Sept. 1973	6 May–13 Aug. 1974	October 1972	October 1973	October 1974
Total seen	190	130	221	232	114	114	192	117
Males	64	47	106	92	36	49	81	50
Females	91	64	92	102	57	53	81	51
Calves	35	19	23	38	21	12	30	16
No. sets twins	5	1	2	4	4	1	0	1
Percentage of females w/ young (after June 1)	33.0	24.6	25.6	43.4	31.5	20.8	37.0	29.4
Calves per 100 adult females[a] (after June 1)	38.5	26.2	28.0	48.7	36.8	22.6	37.0	31.2

[a]Includes yearling females, which at times cannot be distinguished from older moose.

potential calf production. Variations in yearling fertility and twinning rates (see next section) in response to winter conditions may be responsible for annual variations in relative calf numbers on Isle Royale.

NET PRODUCTIVITY AND CALF MORTALITY

Ideally, composition counts from successive fall and winter seasons should indicate the magnitude of calf losses in the intervening period. For Isle Royale moose such records are available for 10 years since 1959 (Table 21). Because of relatively small sample sizes, these percentages are approximate. Year-to-year comparisons have little meaning, but all years can be lumped to provide an average fall and winter calf composition of 17% and 14%, respectively. Since the winter counts were made when calves were 9-10 months old, the average yearling recruitment rate would be somewhat less than 14%—more likely 11–12%. Use of a hypothetical age distribution derived from a life table gives 13% yearlings.

Jordan et al. (1971) calculated annual calf mortality on Isle Royale at 72% using a hypothetical calf crop combined with a 12.5% yearling recruitment rate. High calf mortality is characteristic of moose populations in general. LeResche (1968) estimated moose calf losses in the first 5 months of life in south-central Alaska at 56%. Rausch and Bratlie (1965), working elsewhere in Alaska, found calf mortality ranged from 30% to 80%. Peek (1971a) determined loss between the ages of 5 and 17 months at 24% in mild winter conditions, and 61% mortality in a severe winter in northeastern Minnesota. Heptner and Nasimovich (1967; cited in Peek 1971a) stated that moose calf mortality in the Soviet Union normally ranged between 30% and 50%, but was as high as 80% in some areas. Shubin and Yazan (1959) documented calf mortality of 43% and 66% from the embryo state to 7 months of age in 2 successive years in a Russian moose population.

None of the above authors attributed high calf losses primarily to predation. While wolf predation is implicated at least partially in high calf mortality on Isle Royale, it does not follow that, in the long run, calf survival would increase greatly in the absence of wolves.

LONG-TERM TRENDS IN PRODUCTIVITY

Pimlott (1959) and Markgren (1969) indicated that the twinning rate was correlated with the ovulation rate, and thus was a reliable index to fertility. While Mech (1966) and Shelton (1966) found twinning rates of Isle Royale moose from 1958 to 1963 to be higher than most reported elsewhere in North America, it is clear that the productivity of Isle Royale moose dropped off considerably in the last half of the 1960s and the early 1970s (Fig. 81; Tables 22 and 23). Of 213 cows with young observed during summer in 1959–65, 72 (34%) had twins. The corresponding figure for the period 1966–73 was 33/232 (14%)—a significant decline. Rates

TABLE 21. Proportion of moose calves in successive fall and winter aerial composition counts on Isle Royale (Mech 1966; Shelton 1966; Jordan and Wolfe [unpubl. data]; present study).

	Fall count				Winter count			
Year	Total	Cows	Calves	% calves[a]	Total	Cows	Calves	% calves[a]
1959–60	150	60	33	21.6	529	–	89	16.8
1960–61	28	11	6	21.4	133	–	14	10.5
1961–62	176	61	31	20.3	80	–	14	17.5
1962–63	123	40	15	15.8	128	–	22	17.2
1964–65	171	61	23	15.9	–	–	–	10.0
1965–66	133	67	13	8.8	143	–	13	9.1
1967–68	189	67	33	19.8	151	–	27	17.9
1968–69	233	77	43	21.8	106	55	21	16.0
1972–73	114	53	12	10.2	64	28	6	9.7
1973–74	192	81	30	15.6	113	–	17	15.0
				Average 17.1				Average 14.0

[a]If the number of cows in the sample was available, the percentage of calves was calculated by the following formula: % calves = no. calves/[2 (no. cows) + no. calves] × 100%. Otherwise, % calves = no. calves/total no. moose seen × 100%.

TABLE 22. Twinning rates for Isle Royale moose from summer ground observations.

Source	Year	No. cows w/1 calf	No. cows w/twins	Twinning rate (%)[a]	Remarks
Murie (1934)	1929–30	50	3	6	Very high population (pre-wolf)
Mech (1966)	1959	33	20	38	
Mech (1966)	1960	40	7	15	Considered a "poor" year
Shelton (1966)	1961	37	24	39	
Shelton (1966)	1962	9	3	25	
Shelton (1966)	1963	9	6	40	
Jordan[b]	1964	13	12	48	"Unusually large calf crop"
Jordan[b]	1965	29	9	23	"Below normal"
Johnson[b]	1966	42	2	5	"Subnormal" calf crop
Wolfe[b]	1967	45	9	17	
Wolfe[b]	1968	(29)	(7)	(19)	Fall aerial count
Wolfe[b]	1969	25	3	11	Calf occurrence lower than average
Peterson	1970	25	5	17	
Peterson	1971	17	1	6	Subnormal
Peterson	1972	19	2	10	Subnormal
Peterson	1973	30	4	12	
			Average 1959–65:	34	
			Average 1966–73:	14	

[a]Twinning rate (%) = no. cows w/twins/no. of cows w/calves. In a few instances a calf was seen unaccompanied by a cow. In such cases I assumed that a cow was present and that the calf was a single.

[b]Summer moose observations as reported in unpublished annual project reports.

obtained in this manner should be considered minimal, since ground observations are biased against calves (Pimlott 1959), and there is some loss concurrent with the observations which took place over a period of many weeks.

When Murie (1934) recorded a low twinning rate (6%) on Isle Royale, the moose population was at an all-time high of 2000–3000. The high productivity indicated by the twinning rates in the early 1960s was attributed to intensive wolf predation, which presumably was stimulating reproduction (Mech 1966; Shelton 1966). However, this situation clearly has not been maintained.

Both twins rarely survive their first winter; even by October their numbers have decreased substantially. The percent of twins in fall aerial counts has remained essentially the same during the entire period 1959–74 (Table 23). On Isle Royale a high twinning rate probably contributes little to yearling recruitment, although twins may serve as a buffer against predation on single calves.

The observed drop in twinning rates could reflect lower fertility (ovulation rates), or higher neo-natal mortality. Increasingly severe winter conditions resulting from greater snowfall and an increased moose population may have raised mortality rates of newborn calves by lowering the winter nutritional plane of pregnant cows. Such effects have been reported for most North American ungulates (Swenson 1973). Recent generations of undersized calves (see Residual Effects of Severe Winters) further support this idea. Low twinning rates elsewhere have been attributed to severe winter-spring weather (Knorre 1959) or to low nutritional levels of pregnant cows in winter. (Schladweiler and Stevens 1973; Houston 1968).

Moose Distribution and Habitat Relationships

Early successional stage forests typically support higher densities of moose in North America (Aldous and Krefting 1946; Krefting 1951; Spencer and Chatelain 1953; Peterson 1955). In primeval times and in modern-day wilderness areas fires are the primary factor creating large areas of moose habitat. Social behavior and reproductive characteristics enable moose to exist at low densities in mature forest types and yet increase rapidly to fill expanses of new habitat created by fire (Geist 1974). As forests mature, moose densities shrink in accordance with a reduced food supply. Current high densities of moose on Isle Royale are supported by older, more mature forests, but over time the moose population will decrease unless new burns occur.

Winter Distribution of Moose

Conifer cover becomes more important as snow accumulates in winter, especially if snow interferes with moose mobility. Not only is the snow softer and less

Fig. 81. Calf production declined by the early 1970s.

TABLE 23. Average occurrence of twins in summer and fall, 1959–73.

	Summer ground observation[a]			Fall aerial classification[b]		
Period	Cows w/ one calf	Cows w/ twins	Twinning rate[c]	Cows w/ one calf	Cows w/ twins	Twinning rate
1959–65	141	72	34%	71	7	9%
1966–73	232	33	14%	123	14	10%

[a]From Table 22.

[b]Summarized from Mech (1966), Shelton (1966), and unpublished annual reports of the project, 1965–73.

[c]Significant difference ($t_s = 2.09, P < 0.03$) between the observed summer occurrence of twins in 1959–65 and 1966–73.

Fig. 82. Even in winter moose may seek shade.

Fig. 83. Moose utilize old burns on Isle Royale only with low snow depths.

deep, but snow-covered conifers are effective windbreaks and serve as thermal insulators during cold periods. They may also be cooler in warm periods. Moose often seek shade under conifers in midday, even in winter. With a relatively low surface area:volume ratio and a dark coat, it seems reasonable that moose exposed to full sunlight on calm days in winter could become overheated (Fig. 82).

With average midwinter snow depths of about 60 cm, moose on Isle Royale occur in highest densities in shoreline areas where conifer cover, especially balsam fir, is most common (Figs. 78, 79). Although snow is rarely a serious impediment unless greater than 70 cm deep (Coady 1974a), Peek (1971b: 39–49) found moose moving into conifer cover when snow was only 46 cm deep. Thus snow appears to affect habitat selection even when movements are not seriously restricted.

Recent burns may attract moose in spite of deep snow. The 1936 burn was prime winter habitat in the 1940s (Krefting 1951) and as late as 1957 (Cole 1957). Apparently abundant browse in recent burns compensates for the increased energy expenditure required to inhabit such areas.

Midwinter use of old burns by moose on Isle Royale is affected greatly by snow conditions (Fig. 83). During his census in 1960, Mech (1966) found many moose in burns dating from 1936 and 1948. Snow depths during that census ranged between 30 and 41 cm. Moose were probably more active in open habitats because of low snow levels. During the early 1970s, utilization of these burns was very low, particularly in midwinter. Significant use was last recorded in 1968, when moose were able to move freely about because of little snow (Wolfe and Allen 1973).

The locations of wolf-killed moose also indicate that during periods of deep snow moose leave open burns and congregate in heavy cover near shorelines. With more than 50 cm of snow, there were more kills near shorelines and fewer kills in burns than with less than 50 cm of snow (Table 24).

Cows with calves may instinctively seek denser cover than other moose, presumably because it provides greater protection from wolves. During aerial surveys in Minnesota, Peek (1971a) found that cows with calves were more likely to be found in heavier cover. On Isle Royale, kills of calves are usually near shorelines—in heavy cover—while kills of adults are more randomly distributed (Appendices I-K).

Moose Distribution During Other Seasons

In spring and early summer, moose are often found in aquatic habitat, although little is known of their island-wide distribution pattern (Figs. 84, 85). Botkin et al. (1973) concluded that aquatic plants are the most important source of sodium for moose on the island; they believe that heavy utilization of aquatics is linked to a critical need for this element. Excessive heat and insect pests also may prompt use of aquatic areas (Kelsall and Telfer 1974).

Belovsky et al. (1973:101-122) estimated summer densities of moose on two study areas at the southwestern end of the island indirectly from estimates of

Fig. 84. Cow in beaver pond in late June.

Fig. 85. Cow lying in Lake Superior on hot summer day.

browse production and intake by moose. Their calculated density was 3.8 "adult equivalents"/km^2. The same general area commonly has even more moose in midwinter and probably supports one of the highest year-round densities of moose on the island. Forests in the area are old and relatively undisturbed.

Minimum densities were estimated for some areas of the island from aerial composition counts in October 1974. An area of 18.4 km^2 along the north shore of Rock Harbor, extending from Starvation Point to Lake Richie, contained at least 52 moose, implying a minimum density of 2.8/km^2. This area supports a mature forest dominated by paper birch and aspen, with some balsam fir and white spruce. Most of it was burned shortly before 1846 (Janke 1973). Likewise, densities of moose were quite high in the mature forest of similar composition near Malone Bay. The isthmus between Malone Bay and Siskiwit Lake had a minimum density of 1.7/km^2. Since we made no attempt at a total count, actual densities were undoubtedly higher. By contrast, very few moose were observed in the 1936 burn north of Siskiwit Lake.

Moose-Habitat Relationships

Moose browsing has an obvious effect on the composition of the forest of Isle Royale, reducing or eliminating browse species in some areas. American yew (*Taxus canadensis*), once very abundant, now occurs only where inaccessible to moose. The effect of browsing on forest composition is most striking in the 1936 burn east and south of Lake Richie. Here white spruce—which is not browsed—is rapidly becoming a dominant tree species (Fig. 86). Aspen and paper birch regeneration was greatly retarded and in some cases killed by moose browsing.

Growth form has also been altered by moose. Krefting (1974) found that moose browsing depressed the growth of all favored species—aspen, balsam fir, Canadian honeysuckle (*Lonicera canadensis*), mountain ash (*Sorbus americana*), mountain maple (*Acer spicatum*), paper birch (*Betula papyrifera*), and redosier dogwood (*Cornus stolonifera*) (Fig. 87).

TABLE 24. Effect of snow depth on location of wolf-killed moose.

Snow depth	Kills within 805 m of a lakeshore[a,b]	Kills in burns[c]
Less than 50 cm (n = 47)	47%	31%
Greater than 50 cm (n = 277)	79%	14%

[a]805 m = 0.5 mile.
[b]Significant difference ($t_s = 4.46, P < 0.001$).
[c]Significant difference ($t_s = 2.67, P < 0.001$).

Fig. 86. White spruce, unbrowsed by moose, grows unimpeded in old burns.

Intensive moose browsing actually may prolong browse production in some species. Hazel (*Corylus cornuta*) and redosier dogwood show extensive lateral sprout growth. Both can tolerate heavy browsing and survive. The degree of browsing that a plant species can withstand is quite variable and differs greatly from site to site depending on soil conditions (Bergerud and Manuel 1968). Some aspen- and birch-stands on ridgetops where soils are poor have been killed by browsing, but just off the ridge there are stands of the same species that have grown beyond the reach of moose.

All important browse species except balsam fir show an island-wide downward trend (Krefting 1974). The more rapid, recent changes in the 1936 burn essentially have taken this area out of production of moose browse. Accordingly, moose have shifted from the burn to older forest stands.

Isle Royale continues to support high densities of moose in spite of its old forests. Its insular nature prevents normal dispersal and probably contributes to higher densities than would otherwise occur. The Isle Royale moose population is approximately twice as dense as populations in optimum moose habitat in northeastern Minnesota (Peek 1971a).

The reproductive potential of moose is adapted toward maintenance of the species at low densities in mature forests, rapid expansion into large areas of good habitat following fire, and slow contraction following forest maturation (Geist 1974). The Isle Royale moose population appears to be entering the phase of slow

a

b

c

Fig. 87. Variations in balsam fir growth form are attributable to moose browsing.

contraction. In the absence of fire, their food supply will continue to slowly shrink, leading eventually to a decreased moose population. National Park Service policies are directed toward restoration of a natural fire regime on Isle Royale, with moose densities adjusted accordingly.

Direct Mortality Factors

The Isle Royale moose population has been regulated naturally for its roughly 70-year history, since hunting has never been allowed on the island. From the inception of wolf-moose studies on Isle Royale, emphasis has been placed on the collection of carcasses and skeletal remains in order to determine patterns of natural mortality when moose are preyed upon intensively by wolves.

Calves on Isle Royale exhibit high mortality from year-round wolf predation and to a lesser extent malnutrition and accidents. While significant mortality of newborn calves may occur from uncertain causes, direct predation probably accounts for most mortality after about the first month of life.

As an adult, a moose generally lives for several years with a reduced threat of mortality from wolves, but predation losses increase steadily after 7 years of age. Adult losses occur mainly during winter and early spring. There is evidence suggesting that in late winter, bulls become especially vulnerable. Calves are quite vulnerable when snow is deep. Winter severity has a marked influence on the degree of malnutrition in the population—the record of recent years indicates that malnutrition early in life may account for increased vulnerability of maturing, young adults to wolf predation.

While wolf predation is the primary direct cause of mortality for the Isle Royale herd, accidents and malnutrition also claim some moose. Wolf predation and malnutrition mainly affect calves and old moose, but accidents (including drowning) occur more randomly among adults (Table 25). Since carcass collections are subject to several biases, the frequency of recorded deaths may not reflect mortality in accurate proportions. Calves are undoubtedly underrepresented in all categories because their bones are small and disintegrate rapidly, especially when a calf is very young. Drowning is probably overrepresented because moose that drown and remain floating usually are reported by boaters in summer, so proportionately more of these are examined. Much of the mortality from "unknown" causes probably is attributable to wolf predation.

Wolf Predation on Adults

Wolf kills and probable wolf kills account for 58% (307/531) of the known-age adults in the collection. Most of the known wolf kills listed in Table 25 were first located from the air in winter; probable kills mostly were skeletal remains found during summer field work. The age distributions of adults in the wolf-kill and

TABLE 25. Cause of death for 836 moose, dying of natural causes, examined on Isle Royale, 1958–74.

Age (yrs)	Wolf kill	Probable wolf kill	Malnutrition	Drowned	Other accidents	Unknown
calf	112	107	5	8	6	67
1–2	20	10	2	1	1	13
2–3	11	6	0	3	0	7
3–4	13	4	0	1	1	10
4–5	5	1	0	4	1	11
5–6	4	5	1	0	0	16
6–7	15	6	3	1	2	10
7–8	17	6	1	2	1	18
8–9	12	14	0	0	0	24
9–10	13	13	3	0	0	17
10–11	16	15	0	0	1	22
11–12	13	15	6	0	0	18
12–13	17	14	2	0	0	6
13–14	15	8	1	0	0	6
14–15	7	3	2	0	0	3
15–16	4	2	1	0	0	0
16–17	1	1	0	0	0	0
17–18	1	0	0	0	0	1
18–19	0	0	0	0	0	0
19–20	0	1	0	0	1	0
Total	296	230	27	20	14	249
Mean age[a] (adults)	8.2	9.1	9.8	4.3	7.5	7.9

[a]Adult age assumed to be midway in age interval; e.g., moose aged 7–8 years are considered 7.5 years old.

probable wolf-kill groups are not significantly different ($G_H = 18.18$, 17 d.f., $P < 0.50$). Certainly some of the dead moose in the probable wolf kill group were fed on by wolves subsequent to death from other causes, but the resulting error probably is small (Fig. 88).

Most predation on adults occurs during a relatively short period of time in winter and early spring. While predation in midwinter is often heavier on cows than bulls, the bulls apparently suffer greater losses in later winter and early spring.

Usually, predation is most intensive on older moose, with the rate of loss increasing steadily after 7 years of age; however, the generalization that wolves prey most intensively on older moose has not applied in recent years, when young adults (1+ to 5+ years) accounted for over half of the wolf kills. These moose were apparently vulnerable to wolf predation primarily because of malnutrition early in life, even prior to birth.

SEASONAL ASPECTS

Season of death can be roughly determined for adult males using characteristics of antler development (Table 26). Season of death for females cannot be determined from skeletal remains.

Most bull moose are antlerless for about 4 months, from late December through April. The period of antler development is also 4 months in length (May-August), as is the period with polished antlers (September-late December) (Peterson 1974). Minor fluctuations in this pattern are unimportant. Moose with the largest antlers have begun antler development by the beginning of May, shed velvet early in September, and probably drop their antlers in late December. Moose with smaller antlers, such as yearlings, probably lag behind the larger bulls by at least 2-3 weeks. Losses of adult males are heaviest in winter and early spring. Using the percentages in Table 26, relative rates of adult male mortality are: May-August, 1.0; September-late December, 2.0; late December-April, 12.4. Mortality may be higher among males than females in late winter and early spring due to depleted energy reserves. Therefore, the weighting factor for winter mortality for the total population may be slightly less than 12.4. These figures represent a considerable revision of estimates of Jordan et al. (1971), which resulted in the following relative rates of adult losses: May-August, 1.0; September-December, 1.6; January-April, 1.8.

A rough picture of seasonal patterns of adult mortality can be derived in a different manner, using the occurrence of adult remains in the winter-kill collections versus the summer collections of wolf scats. Adult moose made up 67% (206/307) of the total carcasses from winter studies, 1959-73. In scat collections from the nonwinter period 1973, adults made up only 14% of the total remains of moose; the rest were calves. Adult remains comprised 25% of the classifiable moose remains in fresh summer scats collected from 1958 to 1960 (Mech 1966). While prey occurrence in scats may be affected by biases (Peterson 1974), these data further demonstrate the low vulnerability of adults in the nonwinter months.

Fig. 88. Most adult moose on Isle Royale are eventually killed by wolves.

TABLE 26. Incidence of antlers and antler growth in skeletal remains of male moose on Isle Royale.

Antler condition and estimated time of death	Occurrence in total collection	
	No.	Percent
Antlers still growing, in velvet (May-August)	15	6.5
Antlers polished (September-late December)	30	13.0
Antlers shed, pedicels only (late December-April)	186	80.5
Total	231	100.0

AGE DISTRIBUTION OF KILLS

While wolves prey most heavily on old adults, significant variations in predation patterns over a 16-year period have occurred (Appendix L). Variations in the age distribution of the kill may reflect relative abundance of animals in the older age group and, more recently, increased vulnerability among young adults.

The general pattern. The known wolf kills and probable wolf kills were combined to provide a generalized picture of vulnerability according to age. The relative frequency of kills in each age group was compared to the hypothetical occurrence of each age group in the population (calculated from the life table) to illustrate the differential vulnerability of young and old adults (Table 27).

The marked selectivity of wolf predation is readily apparent (Fig. 89). Mortality, relatively low from age 1 to 5 years, increases after 6 years. After 8 years, the percent occurrence in the kill is greater than the calculated percent occurrence in the population.

Variations in predation patterns. Predation on the young adult group increased dramatically in 1971-73, compared to the early years of the project (Fig. 90). In the mild winter of 1973, moose aged 1+ to 5+ years accounted for 65% (13/20) of the adult wolf kills collected, indicating that the increased vulnerability did not arise from the effects of deep snow on moose mobility. Rather, as records were gathered in successive winters, it appeared that cohorts of calves born after a winter of nutritional distress, or perhaps experiencing such a winter as calves, were permanently more vulnerable to wolves.

Deep snow conditions greatly increased winter severity in 1969, 1971, and 1972, and nutritional distress in the intervening winter, 1970, was evidenced by the small size of calves born the following summer. It is significant that of 13 wolf-killed moose aged 1+ to 5+ years that were killed in 1973, 12 were born after one of these four winters. The other moose was a calf during the deep-snow winter of 1968-69.

In retrospect, the increase in frequency of kills in the group aged 1 + to 5 + years (1959–64:6% to 1965–69:22%) may reflect a slightly increased level of nutritional stress during the 1960s. Increasing trends in population size and snowfall (winter severity) plus a slowly declining food supply because of forest succession combined to cause a progressively lower winter nutritional plane.

While changes in vulnerability are responsible for changes in predation pressure on young moose, relative abundance may have influenced variations in predation on old moose. The majority of adults killed by wolves from 1959 to 1964 were aged 6+ to 10+ years, while from 1965 to 1969 the 11+ to 17+-year-olds were killed most often. In both cases the animals in the age groups most heavily preyed upon were born in a 10-year period, 1947–57. Possibly a series of years with exceptionally good yearling recruitment (calves surviving to age 1) produced a "bulge" in the age structure of the moose population. When these animals became vulnerable, predation may have increased simply because of higher availability.

SELECTION RELATED TO SEX

Mech (1966), Shelton (1966), and Wolfe (in press) found more females than males in their samples of adult moose killed by wolves during the winter—primarily February and March. Since the sex ratio of the herd was probably even, a proportionate number of bulls died at another time, perhaps in late winter and early spring as suggested earlier. While females predominated in winter wolf kills, males predominated among skeletal remains found randomly in summer (Table 28).

TABLE 27. Age-distribution of 307 wolf-killed adult moose compared to hypothetical occurrence in the Isle Royale moose herd.

Age (years)	Wolf-kill sample[a]		Calculated occurrence in moose herd (%)[b]
	No.	%	
1–2	30	9.8	13.1
2–3	17	5.5	12.2
3–4	17	5.5	11.4
4–5	6	2.0	10.8
5–6	9	2.9	10.2
6–7	21	6.8	9.3
7–8	23	7.5	8.3
8–9	26	8.5	7.1
9–10	26	8.5	5.8
10–11	31	10.1	4.5
11–12	28	9.1	3.2
12–13	31	10.1	2.0
13–14	23	7.5	1.1
14–15	10	3.3	0.5
15–16	6	2.0	0.2
16–17	2	0.7	0.1
17–18	1	0.3	0.1
18–19	0	–	–
19–20	1	0.3	–
Total	307		

[a]Includes known wolf kills and probable wolf kills collected during present and previous studies 1958–74.

[b]Calculated from life table (Table 35) (cf. Deevey 1947).

TABLE 28. Percentage of males (± 95% confidence interval) in total sexed remains of carcasses and skeletons of adult moose on Isle Royale.[a]

Method of location	Period of death				
	ca. 1950–60	1960–64	1965–69	1970–74	Total
Wolf kills recorded in winter	20% (5)	35 ± 12% (65)	39 ± 12% (59)	54 ± 12% (65)	42 ± 7%[b] (194)
Summer ground search	60 ± 14% (45)	71 ± 12% (51)	58 ± 13% (57)	54 ± 11% (81)	60 ± 6%[b] (234)
Total	56 ± 14% (50)	51 ± 9% (116)	48 ± 9% (116)	54 ± 8% (146)	52 ± 5% (428)

[a]Sample size in parentheses. Includes only remains for which period of death was assigned.
[b]A proportion was considered to be significantly different from 50% (even sex ratio) if the 95% confidence interval did not include 50%.

PREDATION COMPARED TO HUNTING

Wolf predation represents a natural mortality factor that has shaped survival patterns in moose populations for thousands of years. Predation is usually selective for calves and old moose, and takes equally from each sex in the long run. By contrast, modern hunting of moose in North America takes from all age groups and usually takes more males than females (Cumming 1972; Karns 1972:115–123).

Hunting may lower the percentage of males in a moose population to the point where calf crops suffer. A bull probably fertilizes only one female during the primary breeding period in early October, especially in low-density populations (Fig. 91). Cows that are not bred at this time will again be fertile in 25-30 days, but calves produced from late breeding will be smaller at the onset of winter, which may be critical in harsh environments (Markgren 1974). Additionally, calves born after the peak calving period might be highly vulnerable to wolves in summer.

Hunting is a more random mortality factor—humans tend to remove animals in proportion to their occurrence in the population. The age distribution of hunter kills in Ontario is compared to that of wolf kills on Isle Royale in Figure 92.

Over time, unless harvests are restricted by age and sex, intensive hunting will result in a younger overall age structure, especially among males. Restrictions in Norway and Sweden allow a hunting kill that more closely approximates natural mortality (Bubenik 1972:276–295). Large numbers of prime-breeding-age animals, both males and females, are spared to maximize productivity (Lykke 1974). Similar intensive management in North America is a likely development as human populations and hunting pressure increase throughout moose range.

We should recognize that hunting never could fully duplicate the selectivity that is characteristic of wolf predation. Elimination of wolves probably removes the most important selection force operating on moose populations throughout their evolutionary history, and we should attempt to maintain these natural predators in their ecological role wherever feasible.

Wolf Predation on Calves

Calves comprise the age group most often preyed upon by wolves. The evolutionary significance of predation on calves is readily seen in the development of a strong social bond between cows and their calves during the first year of life. Calves have little defense against wolves, even though they may weigh 3–4 times as much as wolves in winter, so their survival depends on adequate defense provided by their mother (Fig. 93).

Moose calves are preyed upon at all times of the year on Isle Royale. After the first few weeks of life predation is the most important cause of calf mortality. In winter certain snow conditions may increase the vulnerability of calves to wolves.

CALF LOSSES IN SUMMER

Calf mortality is heaviest during the first 5 months of life, when the proportion of calves in the population drops from a hypothetical 31% (Jordan et al. 1971) to 17%

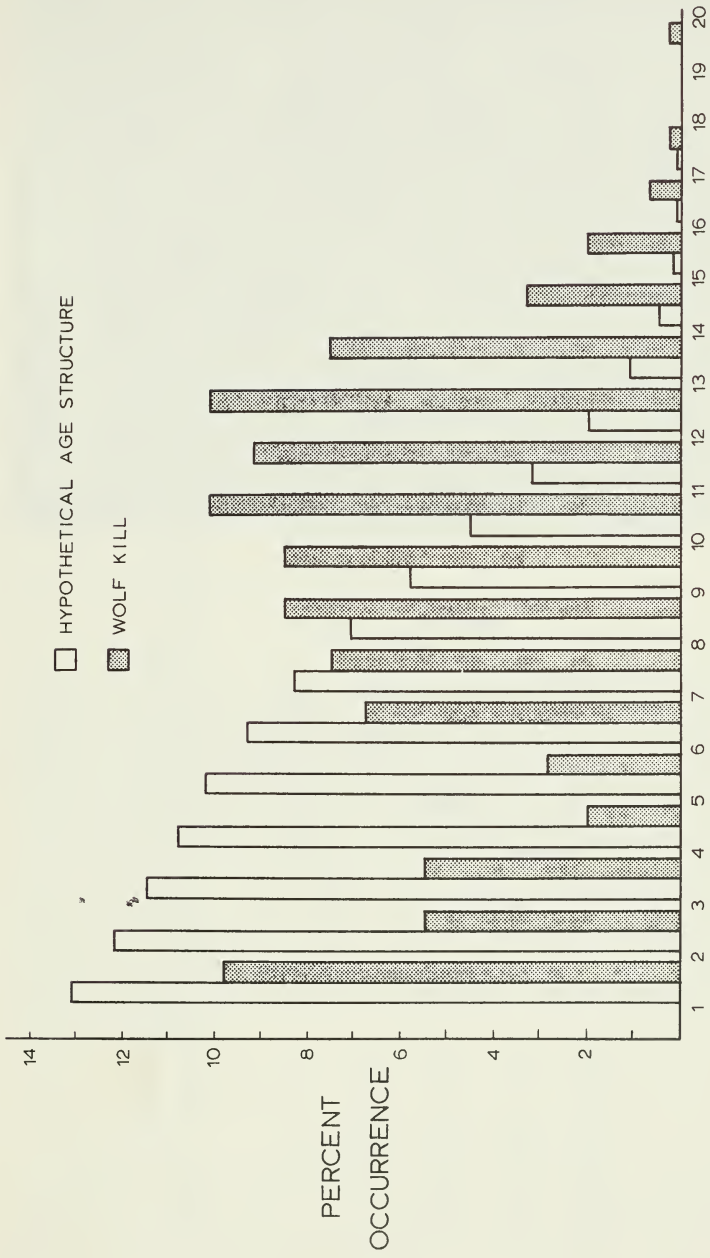


Fig. 89. Age-distribution of wolf-killed adult moose from Isle Royale compared to the hypothetical age-distribution of the population.

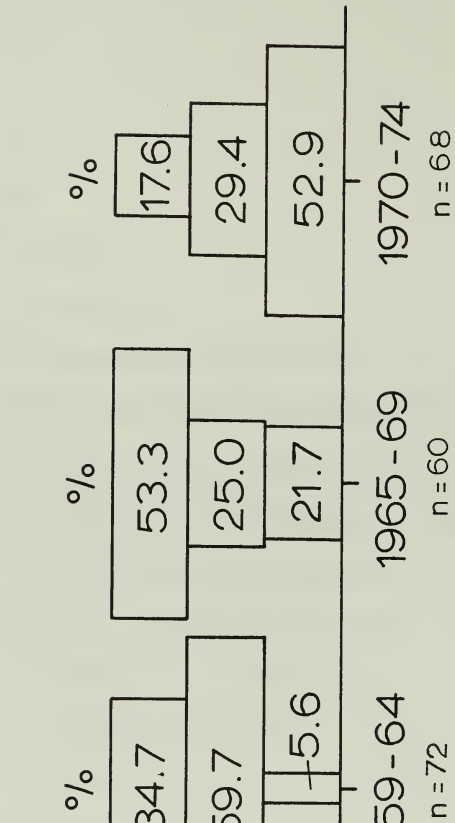


Fig. 90. Temporal variations in age-distribution of 200 adult moose killed by wolves in late January, February, and March on Isle Royale, 1959-74 (see Appendix L for data sources).

Fig. 91. Bull moose following cow during rut.

(Table 21). The causes of this mortality are difficult to document. Twenty-four percent (77/305) of the calves represented in the bone collection were less than 6 months of age. Of these 77 remains, cause of death was recorded as follows: known and probable wolf kills 53%, accidents 12%, unknown 35%.

Calf remains were found in 56% of the wolf scats from nonwinter months in 1973—accounting for 86% of the total identifiable remains of moose. Since young calves seem quite susceptible to malnutrition and accidents, mortality is high whether wolves are present or not. Some of the feeding may simply be scavenging. Occurrence of calves in wolf scats does not decrease during the summer, however, so it seems reasonable to assume that predation causes most of the loss after calves are 1–2-months-old.

CALF LOSSES IN WINTER

Predation causes most calf losses in winter, with known and probable wolf kills totaling 82% (175–213) of the remains of 6- to 12-month-old calves in the bone collection. Winter observations indicate that scavenging is minor relative to direct killing of moose. Calves account for 34% (111/328) of the kills located during 16

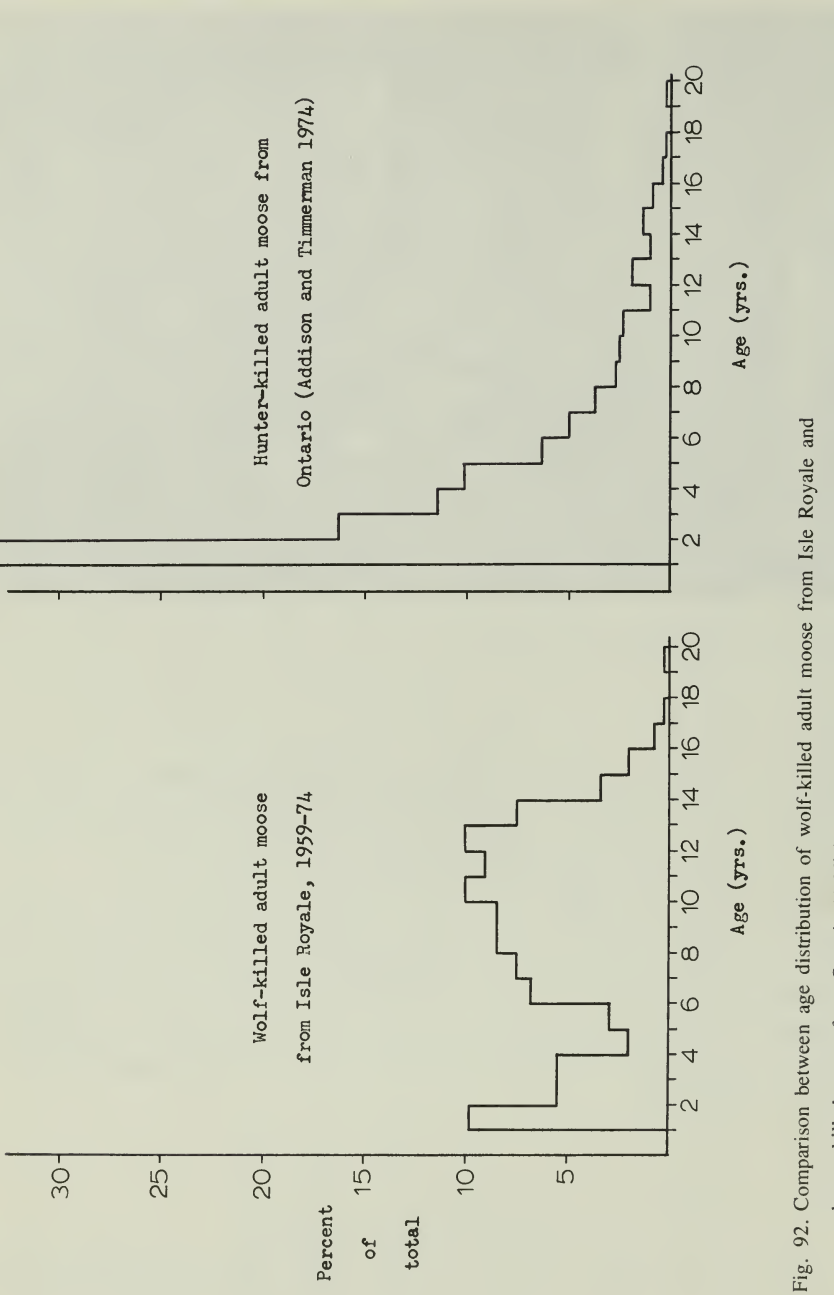


Fig. 92. Comparison between age distribution of wolf-killed adult moose from Isle Royale and hunter-killed moose from Ontario (Addision and Timmerman 1974).

Fig. 93. A calf depends on its mother for protection in the first year of life.

Fig. 94. Calves are more vulnerable to wolves when snow is belly-deep.

winters, but the average proportion of calves in the population during this time of year was estimated at only 14% (Table 21), indicating a marked selectivity.

Snow conditions are extremely influential on calf vulnerability (Fig. 94). During a severe winter in southcentral Alaska, 56% of 57 wolf-killed moose examined were calves (Stephenson and Johnson 1973). On Isle Royale, deep snow made calves especially vulnerable during the winter studies of 1969, 1971, and 1972. Peterson and Allen (1974) commented on the effect of reduced mobility of calves:

> In deep snow a calf finds it easiest to follow in the tracks of its mother. But, when defending their young, cows invariably move to the rear of their calves, providing protection for the area most vulnerable to wolf attack. While this is highly adaptive behavior under normal circumstances, when snow is deep the calf must break trail under a great handicap. This slows the movements of the pair when wolves approach. In 1972, wolves supported by a crust were observed trotting easily beside a calf that was struggling to move through deep snow, protected from behind by its mother. In another case, wolves surprised a cow and calf who were browsing a short distance from one another. They wounded the calf before the mother could come to its aid. In 1971, we recorded two cases of calves probably abandoned on lake edges by their mothers, who may have gone inland to feed.

On Isle Royale snow depths greater than 75 cm, which is about chest height for a 6-month-old calf (82 cm, Kelsall 1969), cause a significant increase in the percentage of calves in the kill (Table 29; Fig. 95).

Snow conditions may adversely affect yearling recruitment. On Isle Royale in October 1972, yearlings totaled only 4.1% of the moose population (Table 19). This low yearling percentage probably resulted initially from low 1971 calf production followed by intensive predation the following deep-snow winter, when calves accounted for 47% of the wolf-killed moose examined ($n = 37$).

There is no conclusive evidence that calf survival is higher without wolves, primarily because comparisons of moose populations with and without predation are invariably complicated by differences in other environmental factors. Calf losses to wolves are not always compensatory, for in some winters wolf predation may cause more mortality than probably would have otherwise occurred (Bishop and Rausch 1974). However, calf survival may be very low even without wolf predation (Houston 1968; LeResche and Davis 1973), demonstrating the potency of other mortality factors.

Malnutrition

Although most important as an indirect cause of mortality, malnutrition may act directly at times. Probably the most significant direct loss of individuals from malnutrition occurs immediately after birth (Fig. 96). Although it is very difficult to determine its actual occurrence, five calves less than 1-week-old were found dead in 1975, probably from fetal malnutrition. Calves may be born weak and underweight, unable to stand and nurse.

Fig. 95. A cow moves to the rear end of her calf when confronted by wolves.

TABLE 29. Effect of snow depth on occurrence of calves in wolf kills.[a]

	Snow depth	
	Less than 76 cm	More than 76 cm
No. of calves	75 (30%)	37 (47%)
No. of adults	172 (70%)	41 (53%)
Total kills	247 (100%)	78 (100%)

[a]Contingency table analysis indicates significant interaction ($\chi^2 = 6.91$, 1 d.f., $P < 0.01$, Siegel 1956).

Twin fetuses have a higher nutritional requirement than a single fetus, so prenatal malnutrition will affect twins the most. One of the five Isle Royale calves found dead in 1975 was known to be a twin. Neonatal mortality was implicated in low twinning rates among Shiras moose (Schladweiler and Stevens 1973). Knorre (1959) mentions several instances of one calf from a set of twins dying soon after birth.

Direct loss to malnutrition in late winter and spring is more easily documented. During the late spring of 1972, which followed a particularly severe winter, I found carcasses of several moose that appeared to have died of malnutrition. Most were near conifer cover, close to lakeshores. The immediate area around the carcass was often depleted of food, indicating that the moose had been there for some time. Most died resting on their sternum, with legs beneath them. Usually their bone marrow was entirely depleted of fat.

Older records list some moose which seem to fit the above description, and for which there was no other obvious cause of death. These are included in the malnutrition group in Table 25. Of 27 such deaths, 19 came from the severe winters of 1970–71 and 1971–72. Calves comprised 26% of the deaths from malnutrition in these 2 years, suggesting a somewhat higher vulnerability in this age class.

The age distribution of adults suspected of dying of malnutrition is skewed toward older animals, as in the wolf-killed sample, and males outnumber females almost 2 to 1. For moose 9 years and older, nearly 3 times as many males die (although the sex ratio derived from Table 35 is 42♂♂:58♀♀). Several studies have shown that bulls, especially those over 2.5-years-old, lose weight during the rut, while females lose little or no weight (Skuncke 1949; Knorre 1959; Yazan 1959). McGillis (1972) found in Alberta that males older than yearlings lost much fat during the rut and were unable to recover this substantial loss before the onset of winter. Because of lower fat reserves, males may be expected to show the effects of negative energy balance before females do.

Most of the known deaths from malnutrition on Isle Royale occurred in late winter. In the spring of 1972, when deep snow lasted well into April, it was obvious that there were more vulnerable moose than the wolves could "cull." Actually, considering the severe conditions, it is somewhat surprising that there was not more direct mortality from malnutrition that year—we found only 12 carcasses in more than 1600 km of hiking.

Direct mortality from malnutrition in late winter is a good indication that the relationship between the moose population and their food supply has changed since the early 1960s. Recent winters of above-average severity or duration, in effect, reduced the carrying capacity of the island to the point where available forage was insufficient to sustain moose in some areas.

Drowning and Other Accidents

Accidents appear to be an insignificant cause of mortality. Except for calves, such mortality appears to be nonselective.

Drowning is mentioned frequently as a cause of mortality among moose. Calves on Isle Royale are more susceptible to drowning than adults, making up 40% of the total recorded. Six of the eight calves were less than 3 months of age. Probably most of these young calves drowned while following their mothers across bays of Lake Superior. High waves may be a factor, since no drowned calves were reported from inland lakes. LeResche (1968), however, reported calves swimming well "in the face of 2-ft waves and high winds." He believed that drowning probably was insignificant after the age of 1 month.

Most of the adults that drowned probably fell through thin ice in early winter or late spring. Two were found in inland lakes, the other 10 were floating in bays of Lake Superior. In females, the approximate date of drowning can sometimes be determined by the relative size of fetuses. A cow that drowned in Rock Harbor contained two well-developed fetuses, indicating death in April (Mech 1966). During a late spring in 1972, the National Park Service boat *Ranger III* reported a cow moose frozen in the ice of Rock Harbor. From fetal development we judged it to have died in February 1972, when ice was just forming. Most drowned adults on Isle Royale were young, corresponding to the higher occurrence of these animals in the population. There is no evident selectivity for older animals, as is the case with some mortality factors.

Most accidental mortality other than drowning is caused by falls (Fig. 97). Three of the 14 carcasses were found in old copper-mine shafts. Four others (including three calves) died of broken legs; one calf had a broken neck. Falls down steep slopes or over precipices and banks accounted for four others. (Five known deaths from falls which occurred during encounters with wolves are listed as wolf kills.)

Ironically, the oldest moose recorded from Isle Royale died accidentally in February 1974. This 19.5-year-old cow fell 5 m from a steep shoreline coated with ice.

There is only one record of a bull moose on Isle Royale dying of puncture wounds incurred during the rut (Hakala 1953). Two others died after locking antlers during the rut in 1968 (Wolfe, in press) (Fig. 98).

Mortality from Unknown Causes

A substantial portion (30%) of the autopsy records list cause of death as "unknown." In most cases these were skeletal remains found months or even years after the actual death of the animal. There are significant differences in the age distribution of wolf-killed adult moose and those dying of unknown causes ($G_H = 37.7$, 17 d.f., $P < 0.01$). Adults in the "unknown" mortality group have a younger overall age structure than wolf kills (32% vs. 16% less than 6 years old,

respectively). Wolfe (in press) concluded from these disparities in age distribution that wolf predation was an unlikely cause of "unknown" deaths. However, the only other mortality factors known to be operating on this moose population are malnutrition and accidents. As previously discussed, malnutrition does not seem to be an important cause of death for the relatively young animals in question; accidents appear to be insignificant.

Thus wolf predation appears to be the only cause of death that could be responsible for losses of such magnitude. Significantly, males predominate in the "unknown" sample (67 ♂♂:33 ♀♀); most of them died between December and April, since 72% had no antlers. This suggests late winter or spring predation, since at that time of year critical malnutrition is more common among males than females. The younger age distribution of "unknown" deaths might result from a late winter-spring increase in moose vulnerability.

Indirect Mortality Factors

Residual Effects of Severe Winters

For moose, food availability is closely related to winter severity. Deep snow restricts movements, reducing energy intake and increasing energy expenditure. Snow conditions are particularly important on Isle Royale, where densities of moose relative to food supply are high. Generally, with deeper snow, moose become more limited to areas of conifer cover near shorelines. This may restrict food consumption or reduce the quality of forage consumed and lead to heavy browsing which may adversely affect future browse production. With deep snow, the kill rates of Isle Royale wolves generally increase, primarily because of greater vulnerability of calves.

Although deep snow could have a direct effect on survival of young adults (Peterson and Allen 1974), the long-term effect of severe winters and associated malnutrition on young moose is more important. Predation increased on moose born after a winter when malnutrition was evident—usually a winter of deep snow. Early growth and development in these moose may have been retarded to the point where survival in subsequent years was lowered (Fig. 99).

In moose, body size at birth is largely dependent on the nutritional status of the mother during the latter part of gestation (Knorre and Knorre 1956; Knorre 1959). Metatarsal length was used in this study as an index of both calf size and the mother's nutritional state during pregnancy. Malnutrition most retards the bones having the highest growth rates during the period of nutritional distress. The major leg bones of young animals show different growth rates—the metatarsus has a higher *in utero* rate of growth, making it the most developed hind limb bone at birth (Peterson 1974). Metatarsus length of domestic lambs up to 10-months-old was correlated with prenatal nutritional plane and depended very little

Fig. 96. Calves may die of nonpredatory causes soon after birth.

Fig. 97. Injuries, such as this broken leg, may predispose moose to predation.

Fig. 98. These two bulls drowned in a beaver pond after locking antlers, a rare occurrence during the rut.

on postnatal nutrition (Palsson and Verges 1952); this also was assumed true for moose. Extensive collections were possible only from 9- to 10-month-old calves. Fortunately, wolves commonly left the lower hind leg (the metatarsus) intact.

The collection of calf metatarsi began in the winter of 1971 and continued through the study. These were used to compare calves born in different years (Table 30). Analysis of variance (model *II*) indicates significant differences between cohorts ($P < 0.025$). Mean metatarsal length increased in each succeeding year, with the greatest jump occurring in 1973. A multiple comparison test (Newman-Keuls) indicates that the metatarsi of the 1973 calves were significantly longer than those of the 1970 and 1971 calves ($P < 0.05$).

In addition to fetal malnutrition, a delayed birth (because of delayed estrus) might cause shorter metatarsal length in a moose calf killed in its first winter. Late breeding would be expected most often among yearling females (Coady 1974b). However, because of their low winter nutritional plane we would expect few Isle Royale yearlings to be breeding. Additionally, calves born late would be highly vulnerable to wolves in summer and few would survive until winter.

Fig. 99. Abnormal antlers of 2.5-year-old moose killed by wolves in 1972.

TABLE 30. Mean metatarsal length (in mm) for 6- to 12-month-old moose calves according to year of birth.

	Year of Birth			
	1970	1971	1972	1973
Mean metatarsal length ± 95% conf. interval:	319 ± 4.8	322 ± 5.9	326 ± 7.1	332 ± 5.4
Sample size:	20	21	11	11
Inter-year difference:				
1970	–			
1971	3	–		
1972	7	4	–	
1973	13[a]	10[a]	6	–

[a]Significant difference between cohorts, Newman-Keuls test ($P < 0.05$).

In 1972, we extended the collection of metatarsal to provide baseline data for all ages of moose (Table 31). Little increase in metatarsi length occurred after 4 years of age, so these animals were placed in one group. Metatarsal length in females

generally averaged slightly less than in males, but the difference was statistically significant ($P < 0.03$, t-test) only in the relatively large sample from moose more than 4-years-old.

The age at which epiphyseal union occurs provides another indicator of growth. Between the epiphysis (the bony cap at the end) and the metaphysis (main shaft) of long bones is a layer of cartilage—the center for longitudinal bone growth. After growth has been complete, the cartilage is replaced by bone, which fuses the epiphysis to the main shaft.

Studies of black-tailed deer have shown that deficient diet could delay epiphyseal fusion for at least 12 months, and that fusion of metatarsal epiphyses in this species occurs by 27–29 months of age (Lewall and Cowan 1963).

Epiphyseal closure in moose metatarsi can also occur as early as 29 months of age (Table 31). Thus, 9 of the 17 wolf kills between 2 and 4 years-old (seven, 2–3 years old and two, 3–4 years old) suffered obvious growth retardation. These young adults were born in years when calves were undersized at birth, indicating a long-term vulnerability resulting from early malnutrition.

Factors Affecting Adult Vulnerability

Increased age is an obvious liability to moose on Isle Royale. Of special interest, then, are pathological conditions associated with advanced age. Usually, examination of wolf-killed moose is limited to well-chewed skeletal remains, making it impossible to check for abnormalities in soft tissues. Even so, bone abnormalities (arthritis, jaw necrosis, severely fat-depleted bone marrow, or broken bones) were found in a high percentage (38% of 205) of wolf-killed adults examined, 1958–74. Arthritis and jaw necrosis are rare among moose less than six years old. Arthritis and malnutrition affects males much more than females, probably contributing to some differential mortality between the sexes. In addition to bone pathology, a high load of parasites may increase vulnerability in some moose.

ARTHRITIS

Arthritis, through restricted mobility, probably plays an important role in increasing the vulnerability of moose to wolf predation (Fig. 100). The arthritic lesions observed in Isle Royale moose closely resemble osteoarthritis, or degenerative joint disease (Neher and Tietz 1959; Stecher 1963). Sokoloff (1969:2) defines this condition as a "noninflammatory disorder of movable joints characterized by deterioration and abrasion of articular cartilage, and also by formation of new bone at the articular surface." This type of arthritis occurs primarily in old individuals and is most common in weight-bearing joints. Among Isle Royale moose, arthritis was found most frequently in the hip (Table 32).

Arthritis is usually not evident before 7 years of age in either sex, but after this age is attained the overall incidence in males is significantly greater than in females

TABLE 31. Mean metatarsal length (mm) of Isle Royale moose (primarily wolf kills).[a]

	At birth	1–6 mo.	6–12 mo.	12–18 mo.	18–24 mo.	2–3 yrs.	3–4 yrs.	4+ yrs.
Males	223(1)[b]	–	329(17)	334(2)	357(7)	360(5)	365(4)	374(49)[c]
Females	220(1)	290(1)	325(21)	343(1)	357(3)	349(3)	367(4)	369(46)[c]
Unknown sex	–	281(6)	322(32)	–	–	371(1)	–	369(4)
Mean	222(2)	282(7)	325(70)	337(3)	357(10)	355(9)	366(8)	371(99)
95% conf. interval for mean	± 19	± 16	± 4	± 16	± 15	± 19	± 25	± 2
% showing epiphyseal union	0	0	0	0	0	22	75	100

[a]Mean length for moose older than calves is minimal, since wolves are mainly limited to relatively inferior adults.
[b]Sample size in parentheses.
[c]Sex difference significant at $P < 0.02$ ($t_s = 8.00$, 93 d.f.)

Fig. 100. Normal vs. arthritic pelvic joint of moose.

(Fig. 101): 40% of 102 males compared to 13% of 88 females ($t_s = 4.47$, $P < 0.001$). While arthritis is often a normal consequence of aging, the differences between males and females pose several interesting questions about arthritis which research has not yet answered.

JAW NECROSIS

Necrotic lesions of the bone surrounding the cheek teeth of older moose were often found (cf. Murie 1934; Mech 1966; Shelton 1966). This seems to be a chronic infection caused by microorganisms that gain entrance to the soft tissues surrounding the teeth.

It is probable that microorganisms responsible for jaw necrosis in moose are universally present in the oral cavity. Entrance into the soft tissues of the jaw can be gained through any opening. The molariform teeth of a moose wear down considerably with age, and necrotic lesions commonly develop when the tooth surface is worn to or below the gum line (Passmore et al. 1955). Food that becomes

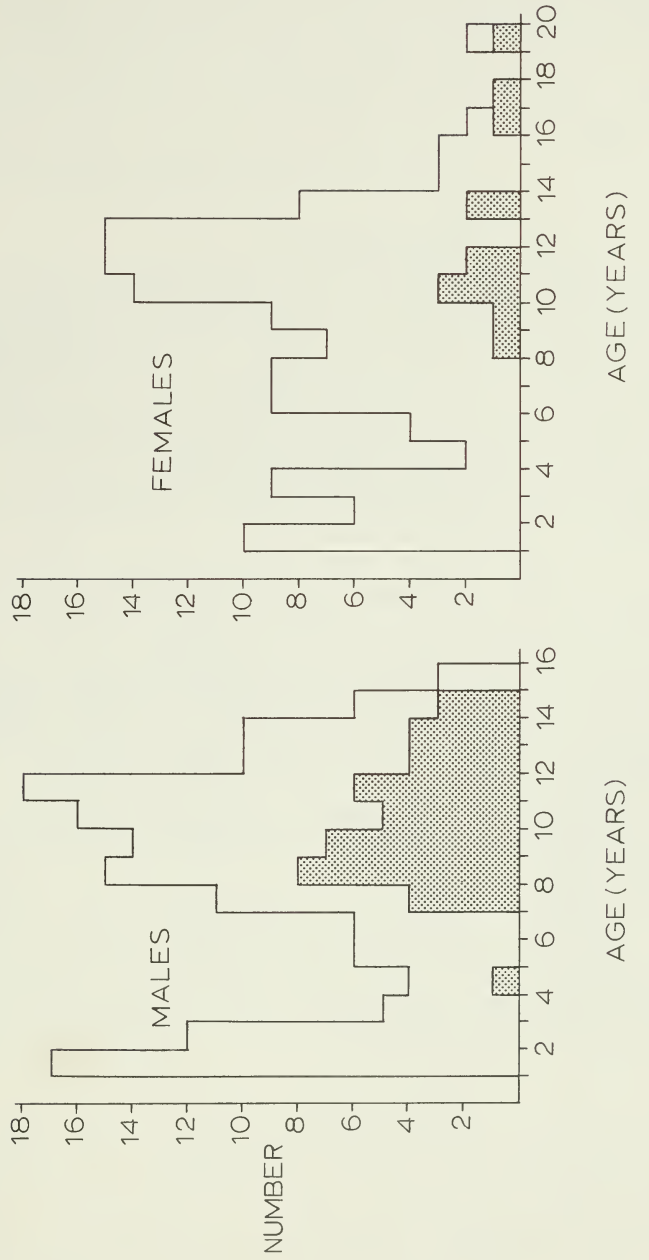


Fig. 101. Incidence of arthritis in the coxofemoral (hip) joints of moose dying on Isle Royale.

impacted between teeth or around their base may also provide a focus for infection (Fig. 102). The infection may spread to the entire toothrow or remain localized. In severe cases, teeth may loosen and fall out, and, in rare cases, the jaw may break.

Jaw necrosis is limited to older individuals, and the incidence of necrotic lesions is directly related to age (Fig. 103). Of 344 adults over 7 years of age, 25% had some jaw pathology at death. Ten percent showed severe necrosis (loss of teeth or massive bone necrosis.

MALNUTRITION

Moose suffering from malnutrition are undoubtedly more vulnerable to wolf predation. Moose with class 3 bone marrow probably had seriously depleted their energy stores. This may be a conservative estimate, since some marrow placed in the class 2 category had very low actual fat content.

Bone-marrow condition was noted for 269 wolf-killed moose (including probable kills) during 1958-74 (Table 33). All calves and almost all of the adults were killed in winter, usually during January, February or March.

The percentage of calves with serious fat depletion (45%), 1970-74, is significantly higher than for 1958-69 (21%) ($t_s = 2.21$, $P < 0.03$). During the recent period, marrow fat of calves was quite variable but correlated to a certain extent with winter severity. In 1969-70, (a winter of apparent nutritional distress) all four calves examined had severely depleted bone marrow. During the difficult winters of 1970-71 and 1971-72, of the calves examined, severely depleted marrow was present in 59% (13/22). By contrast, none of the 10 calves examined during the mild winter of 1972–73 had severe marrow fat depletion. Of 11 calves examined, 1973–74, 27% had severely depleted marrow. These samples are small, but they provide some indication of the effect of winter conditions on calf welfare.

The low incidence of fat-depleted marrow in wolf-killed adults in 1970–74 resulted from the large number of young adults in the sample. All these animals had normal bone marrow.

Males are more susceptible to death from malnutrition than females, as discussed previously. The incidence of severe marrow-fat depletion in adult males (21% of 78 kills) was significantly higher than in adult females (9% of 103 kills) ($t_s = 2.27$, $P < 0.03$). Like arthritis, malnutrition apparently contributes to a differential mortality between males and females.

PARASITES

The incidence of parasites in Isle Royale moose is difficult to document, since soft tissues are rarely available for examination. Nevertheless, since wolves are sensitive to slight changes in the health of a moose, heavy parasite loads might contribute to increased vulnerability. Parasites may be quite innocuous in healthy hosts, but they constitute a greater liability with increased age and reduced vigor.

TABLE 32. Site of arthritic lesions in Isle Royale moose.

Location	Sex			
	Male	Female	Unknown sex	Total
Coxofemoral joint	39	11	2	52
Scapulo-humeral joint	2	0	0	2
Vertebrae	4	0	3	7
More than one site	2	2	1	5
	47	13	6	66

TABLE 33. Incidence of fat-depleted bone marrow in Isle Royale moose killed by wolves, 1958–74.

Time period	Calves		Adults	
	Incidence of fat depletion[a]	Sample size	Incidence of fat depletion[a]	Sample size
1958–64	16%	25	18%	71
1965–69	29%	7	22%	41
1970–74	45%	42	5%	83
Total sample	34%	74	13%	195

[a]Class 3 bone marrow.

In addition to two common ectoparasites—moose fly (*Lyperosiops alcis*) and winter tick (*Dermacentor albipictus*)—three internal parasites were noted during early Isle Royale investigations: a lungworm (*Dictycaulus hadweni*) and cysts of two tapeworms (*Echinococcus granulosus* and *Taenia hydatigena*) (Murie 1934; Mech 1966). Jordan (unpubl. data) found two additional organisms: *Sacrocystis* (a fungus) and *Nematodirus* (an intestinal nematode).

According to Mech (1966), heavy infestations of ticks are often found on animals in poor condition and in some populations are an important, direct cause of death (Fig. 104). Ticks cause irritation sufficient to make moose scratch and rub their hides, even with their teeth, often resulting in hair loss in areas of heavy tick infestation. Mech (1966) suggested that irritation from ticks accounted for bare areas seen on moose in spring. However, since the bare areas on the upper back and neck correspond to those where winter hair is first shed, this loss of hair in spring is more likely a molt pattern. Such bare areas are rarely seen in Alaskan moose (A. Franzmann, pers. comm.), indicating an unusual condition on Isle Royale.

While it is often possible to state whether ticks were present on an animal killed by wolves, the importance of such infestations cannot be determined in most cases. There is little evidence that ticks are a primary factor predisposing Isle Royale moose to wolf predation. However, in some cases ticks may act with other influences to increase vulnerability.

Hydatid cysts. The internal parasite of Isle Royale moose which seems the most important is *Echinococcus granulosus*. Cysts of this parasite contain the larval stage, hundreds of tiny protoscolices, each of which is capable of developing into an adult tapeworm if eaten by a definitive host (Smyth 1964). Cysts are usually found in the lungs, occasionally the liver, and were found once in a kidney (Shelton 1966) (Fig. 105). They commonly reach an inch in diameter.

The only definitive host for this parasite on Isle Royale appears to be the wolf (Peterson 1974). The mature tapeworm develops in the intestine of wolves; eggs are shed with the feces. The eggs are somehow ingested by moose, and the cycle is completed as the larval stage migrates to the lungs and liver via the bloodstream, finally forming a hydatid cyst (Smyth 1964).

In an individual moose, hydatid cysts apparently accumulate with age, as shown by other studies (reviewed by Mech 1966) and by data gathered by the many investigators involved in Isle Royale wolf-moose studies since 1958. In a sample of 32 moose, those older than 3 years of age had at least a few hydatid cysts (Table 34). Older moose on Isle Royale probably all harbor *E. granulosus*.

After reviewing several studies of the effects of hydatid cysts on the health and vigor of ungulates, Mech (1966) concluded that, in a stressful situation such as a wolf attack, a heavy load of hydatid cysts could increase the vulnerability of a moose. Under persistent attack by wolves, even a slight impairment in the ability of the moose to escape probably is significant. (At the same time, the parasite increases the possibility of transmission to the definitive host, thus completing its own life cycle.)

a

b

Fig. 102. Jaw necrosis in Isle Royale moose, apparently resulting from (a) excessive wear, and (b) food impaction.

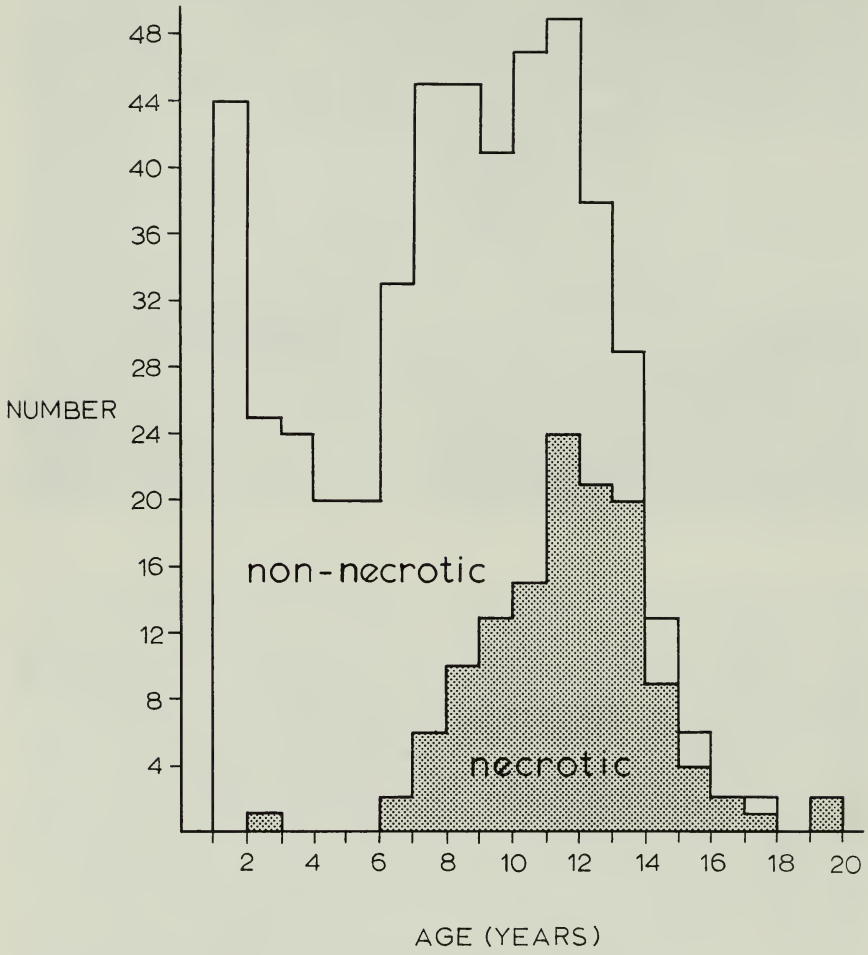


Fig. 103. Incidence of jaw necrosis among moose dying on Isle Royale.

Life Table for Isle Royale Moose

Life tables are a valuable means of summarizing mortality patterns in relation to age. Mech (1966) and Shelton (1966) used a life-table approach, based on age according to toothwear, to analyze mortality patterns in the Isle Royale moose herd. Wolfe (in press) constructed a life table for the same population based on collections through 1969 using the more accurate cementum annulations method. Because major shifts have occurred recently in the mortality of certain age groups, and sampling of year-round mortality has greatly increased since 1970, a new life table has been constructed. This life table, based on carcass collection spanning the period 1958-74, should result in a more realistic representation of long-term mortality patterns in the Isle Royale moose herd.

TABLE 34. Incidence of hydatid cysts in lungs of Isle Royale moose.[a]

Age	No. sampled	No. infected	No. cysts
0–3 mos.	3	0	–
6–12 mos.	4	0	–
1+ yrs.	4	1	8
2+ yrs.	4	2	1, 15
3+ yrs.	2	2	9, 18
4+ yrs.	2	2	4, 14
5+ yrs.	1	1	4
6+ yrs.	2	2	15, 57
7+ yrs.	4	4	2, 15, 38, 40
9+ yrs.	1	1	25
10+ yrs.	2	2	21, 35
11+ yrs.	1	1	50
13+ yrs.	1	1	80
14+ yrs.	1	1	74
	32		

[a]Sample includes moose checked by all investigators since 1958.

Fig. 104. Male tick (second from left) and three female ticks in varying stages of engorgement with moose blood (scale in centimeters).

Fig. 105. Hydatid cysts in moose lung.

Techniques

The life table for Isle Royale moose was constructed according to methods described by Deevey (1947) and Caughley (1966). Included are estimates of the following parameters:

(1) Mortality (d_x): the number of deaths within the age interval x to $x + l$. This is determined from the proportion of recorded deaths in an age interval to the total deaths recorded for all ages, applied to the initial cohort size (usually 1000).

(2) Mortality rate (q_x): the proportion of a cohort dying between age x and $x + l$, This is determined by dividing d_x by l_x.

(3) Survivorship (l_x): the probability of an individual surviving from time of entry into the table to any age x. Usually l_x is multiplied by a constant $K = 1000$. Then the l_x series indicates the number alive at any subsequent age.

Since natality rates for Isle Royale moose are unknown, I did not attempt to combine mortality rates with estimates of fecundity to arrive at an estimate of age distribution. Instead, I calculated the "L_x" statistic (Deevey 1947), which is simply an average of successive "l_x" figures. This is the hypothetical age distribution at a point midway in each age interval, assuming equal recruitment each year and constant mortality rates.

I have assumed that the aggregation of records from all sources adequately represents year-round mortality patterns in the Isle Royale moose population over roughly the last two decades. Data on sex, age, and approximate time of death for the specimens used for the analysis are provided in Appendix M. In addition, 54 skeletons that could not be assigned to a specific 5-year period were included in the life-table calculations.

Possible Biases

While simple in principle, the construction of life tables for wild populations may be complicated by various difficulties (Caughley 1966; Eberhardt 1969). If a life table is calculated from mortality data spanning several years, it is necessary to make the assumption, often untenable, that population size and age structure have remained stable during those years. Sampling must adequately represent mortality during the entire year. Small sample sizes in each age interval may be a problem with long-lived animals. An accurate method of age determination is necessary. Survivorship curves made by plotting successive "l_x" values may not be representative of a population when derived from "time-specific" records, since there are variations resulting from unusually high survival or mortality in particular cohorts (Bubenik 1972:276–295; Collier et al. 1973).

I must assume that population size and age structure have remained relatively constant during the period of collection. Caughley (1966) stated that the error introduced by population fluctuation probably is insignificant if the period of collection exceeds the average wave length of the fluctuations; under such condi-

tions variations in mortality would be compensatory. Because there have been some population changes, the life table will be biased to the extent that fluctuations in population levels and mortality patterns are not compensatory—thus the current life table for Isle Royale moose is only an approximation of population parameters.

The total skeletal collection was used as the data base for the life table. Initially, the data derived from moose found during random summer ground searches were used. However, the 60 ♂♂:40 ♀♀ sex ratio in the random collection indicates inadequate sampling for all seasons, since the actual sex ratio has probably varied little from equality. It is true that in the total collection the January-March period is more heavily sampled than April-December, but exclusion of the winter-spotted kills would result in more bias than when they are included. Since many of the remains of moose found during winter aerial searches would have been found during later random searches, the entire collection appears to be the least biased representation of year-round mortality.

Since the entire collection spans 25 years there is little reason to believe the data are biased by a year, or even a series of years, of unusual calf production or survival. Possible sex bias stemming from differential ease in finding remains appears insignificant (Peterson 1974). Calves, especially those 1-6 months old, are certainly underrepresented in the skeletal collection, so the life table has been constructed for the adult segment of the population only. The estimate of calf mortality by Jordan et al. (1971) is incorporated into the survivorship curve.

The Life Table

Life table series were calculated for adult males, females, and combined sexes (including moose of unknown sex) (Table 35). The resulting survivorship curve illustrates the age-selectivity of wolf predation—the major mortality factor for adult moose (Fig. 106). This curve would be a straight line if mortality rates were constant for moose of all ages. Using this curve we can follow the fate of a hypothetical cohort of 1000 yearlings. Moose that have survived their first year of life have a mean life expectancy of 7.3 years. Between the ages of 1 and 7 years, annual mortality rates are about 10% or less; rates increase steadily thereafter. Males have essentially died out by age 15.5 years, females by age 19.5.

The mortality rate for Isle Royale moose (Fig. 107) shows the same "U"-shaped pattern that Caughley (1966) found typical of a wide variety of mammals, ranging from laboratory populations of rats and voles to wild and domestic ungulates. Similar mortality trends in African ungulate species have also been reported (Spinage 1970, 1972).

Calves averaged 14% of the population in mid-winter on Isle Royale; yearling recruitment was estimated at 11–13%. Average annual adult mortality was calculated at 13% (Table 35).The similarity between these figures suggests long-term stability in the moose population. This does not imply that substantial fluctuations

TABLE 35. Life table for Isle Royale moose.

Age (years)	Males					Females					Total				
	No. of remains	d_x	l_x	q_x	L_x	No. of remains	d_x	l_x	q_x	L_x	No. of remains	d_x	l_x	q_x	L_x
1–2	28	108	1000	0.108	946	16	74	1000	0.074	963	47	88	1000	0.088	956
2–3	16	62	892	0.070	861	9	42	926	0.045	905	27	51	912	0.056	887
3–4	12	46	830	0.055	807	12	56	884	0.063	856	29	55	861	0.064	834
4–5	12	46	784	0.059	761	8	37	828	0.045	810	22	41	806	0.051	786
5–6	13	50	738	0.068	713	7	32	791	0.040	775	26	49	765	0.064	741
6–7	12	46	688	0.067	665	21	97	759	0.128	711	37	70	716	0.098	681
7–8	20	77	642	0.120	604	15	69	662	0.104	628	45	85	646	0.132	604
8–9	30	116	565	0.205	507	15	69	593	0.116	559	50	94	561	0.168	514
9–10	22	85	449	0.189	407	19	88	524	0.168	480	46	86	467	0.184	424
10–11	26	100	364	0.275	314	21	97	436	0.222	388	54	102	381	0.268	330
11–12	29	112	264	0.424	208	20	93	339	0.274	293	52	98	279	0.351	230
12–13	15	58	152	0.382	123	23	106	246	0.431	193	39	73	181	0.403	145
13–14	14	54	94	0.574	67	15	69	140	0.493	106	30	56	108	0.519	80
14–15	7	27	40	0.675	27	6	28	71	0.394	57	15	28	52	0.538	38
15–16	3	12	13	–	7	3	14	43	–	36	7	13	24	0.542	18
16–17	–	–	–	–	–	2	9	29	–	25	2	4	11	–	9
17–18	–	–	–	–	–	2	9	20	–	16	2	4	7	–	5
18–19	–	–	–	–	–	–	–	11	–	11	–	–	3	–	3
19–20	–	–	–	–	–	2	9	11	–	6	2	4	3	–	2
TOTAL	259					216					532				

Average annual adult male mortality (q_x) = 0.133.
Average annual adult female mortality (q_x) = 0.120.
Average annual adult mortality (q_x) = 0.128.

Average life expectancy of males at age 1 year (e_l) = 7.02 years.
Average life expectancy of females at age 1 year (e_l) = 7.81 years.
Average life expectancy at age 1 year (e_l) = 7.28 years.

could not have occurred. The calculated average mortality rate is rather insensitive to small differences between recruitment and mortality which could, over a period of several years, lead to considerable population change. A large difference between recruitment and mortality in a single year could also result in a significant population change but would not be reflected in these statistics.

Sex Difference in Survival

Isle Royale bulls have not been found to live longer than 15.5 years, while cow moose have lived as long as 19.5 years. Males of a given age tend to have a slightly higher mortality rate than females of the same age (Table 35). The greater incidence of malnutrition and arthritis in bull moose has already been discussed. Sex differences in survival, while apparently real, are not sufficient to significantly alter the calculated age distribution of males and females, even when only the oldest age groups (11 + years and up) and compared (G_H = 12.3, 8 d.f., P <0.15). Larger sample sizes are needed to confirm a small difference in survival.

From the age distribution (L_H, Table 35) of the moose population the proportion of males in each age interval was calculated (Fig. 108). The sex ratio remains essentially even from ages 1-8. After age 8, the proportion of males drops gradually for several years, with the rate of decline accelerating in the oldest age classes. The proportion of males does not fall below 45% until after 10 years of age. Since only about 12% of the population is calculated to be older than 10 years, differential mortality in males and females has little effect on the sex ratio of the entire population.

Higher mortality rates are common in males of various ungulate species. The reasons suggested for disproportionate male mortality include greater growth rates in males and stress during the rut, when male activity is greatest and food consumption drops markedly (Robinette et al. 1957; Borg 1970; Flook 1970). These factors may explain the greater incidence of malnutrition among bull moose on Isle Royale. Since wolves are capable of detecting slight incapacities, arthritis is probably an important additional reason for a shorter average lifespan among males.

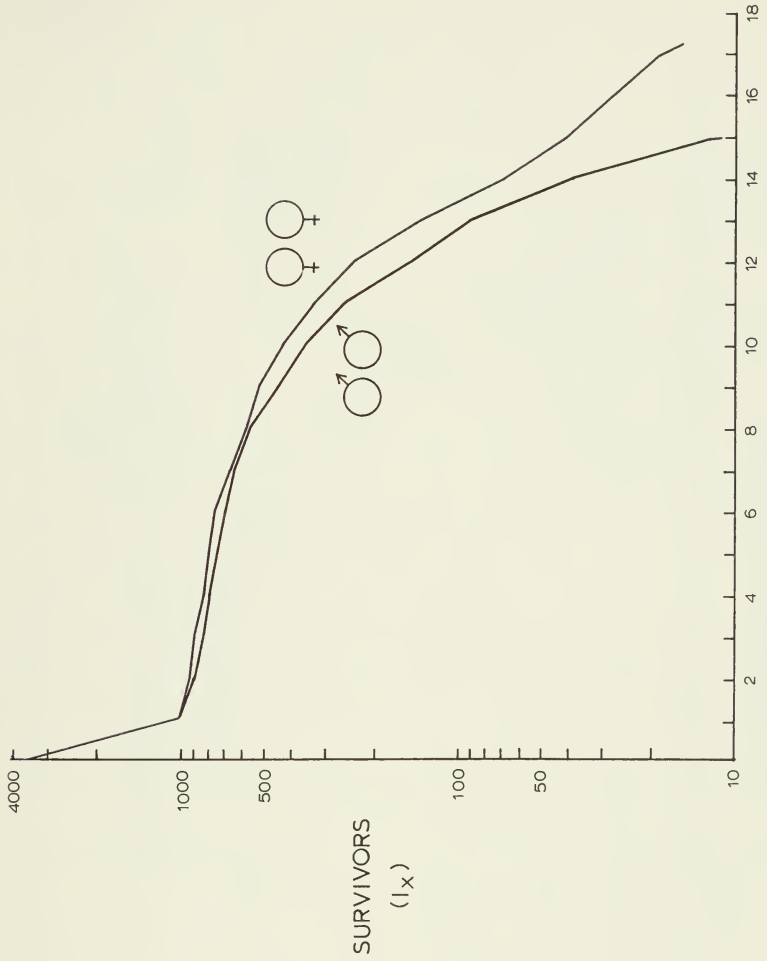


Fig. 106. Survivorship curves for male and female adult moose on Isle Royale.

Fig. 107. Age-specific mortality rates for Isle Royale moose.

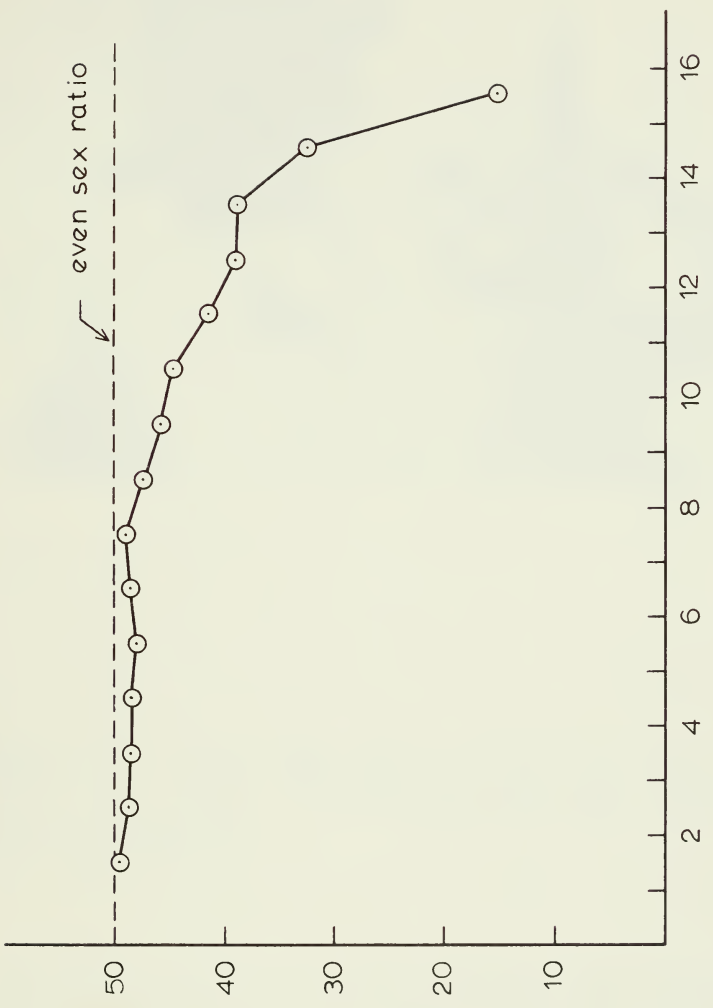


Fig. 108. Calculated proportion of males alive in each age interval, based on a hypothetical age distribution for adult moose on Isle Royale.

4
Moose and Wolves in an Island Ecosystem

In biological communities, homeostatic mechanisms evolve which increase the efficiency of energy use in the ecosystem (Watt 1970). Larger numbers of species in any given system contribute to more complex energy pathways and thus promote stability (MacArthur 1955).

Islands may have only a limited number of species, and because of this inherent simplicity fewer stabilizing mechanisms exist and fluctuations in populations are more likely to occur. Because dispersal is limited, island populations may reach higher densities than mainland populations of the same species. Conclusions drawn from ecological studies on islands must always recognize these unique characteristics.

Moose Population Regulation

During the present wolf-moose studies on Isle Royale (1970–74) it was clear that food supply played a major role in moose population dynamics, as evidenced by reduced calf production and increased signs of malnutrition compared to a decade earlier, when calf production was high and there was no evidence of limitation by food supply. It appeared at that time that intensive wolf predation was ". . . maintaining the moose population below the level at which food would restrict it" (Mech 1966:167). This initial interpretation has now been revised.

In spite of imprecise population estimates, there were indications of an increase in moose numbers during the 1960s. Certain environmental factors, influential during the same period, partly account for changing relationships in the browse-moose-wolf complex. Burns which formerly contained abundant moose browse became less important to moose as forest succession continued. Since the early 1960s significant utilization of these burns has been limited to winters of little snow and unrestricted mobility for moose; in recent years (1969–74) high moose densities had to be supported in more mature forest types. Recent severe winters have emphasized the influence of environmental factors on condition and, ultimately, on population levels of moose.

In response to changes in moose vulnerability, wolf predation began to increase in 1969, especially on calves and young adults. Kill rates generally were high, carcasses were underutilized, and a second pack of wolves became firmly established on the island for the first time since these studies began.

Although Pimlott (1967) suggested that highly developed intrinsic forms of population regulation have not evolved among North American ungulates because of intensive predation throughout their history, moose do exhibit important responses to environmental influences which introduce a degree of intrinsic control to population levels. Since moose are not highly preferred prey of wolves when smaller ungulates are available (Murie 1944; Pimlott et al. 1969; Mech and Frenzel 1971), buffer species could have reduced the potential effect of predation on moose during their evolutionary development and therefore resulted in moose effective intrinsic controls. Social behavior which effectively disperses a moose population may prevent high densities when the food base is inadequate. Agonistic behavior apparently spaces moose efficiently throughout their habitat and contributes to their solitary social organization (Houston 1974), although moose may congregate where food is abundant (Geist 1974). Furthermore, sexual maturity in adult moose may be delayed by at least a year in response to a reduced food intake in the first year of life, and calf production and early survival are related to nutrition (Pimlott 1959; Markgren 1969). Thus, the growth potential of a moose population is adjusted to the nutritional level, allowing a rapid increase when densities relative to available food are low, and exerting a stabilizing influence as food supply becomes more limiting.

Irruptions of moose populations, followed by catastrophic losses to malnutri-

Fig. 109. Wolf predation is essential to the healthy maintenance of a high moose population on Isle Royale.

tion, are rather rare. The case which is most often cited is that of Isle Royale in the early 1930s. However, the insular nature of this ecosystem, the lack of predation, and an abundant source of food that was highly sensitive to moose browsing (evidenced by the elimination of *Taxus canadensis* [American yew] as a shrub species) presented a unique set of ecological circumstances. Some naturally regulated moose populations, in the absence of predation, have stabilized without heavy losses (Houston 1968; LeResche 1970), supporting the hypothesis that moose have evolved some effective intrinsic controls.

The effect of climatic conditions such as snow cover (an extrinsic factor) may be determined largely by population density. Snow of a given depth, for example, may introduce more nutritional stress to Isle Royale moose than to mainland populations because of higher densities on the island. In Alaska the influence of snow on moose varied with moose densities and habitat quality (Bishop and Rausch 1974). Snow conditions are an important element in the environmental framework within which moose and wolves interact.

There appear to be no adequately documented cases of wolf predation imposing a long-term limit on ungulate populations independent of environmental influences. However, wolf predation is probably the most efficient natural mortality factor capable of altering prey population levels in response to food and climatic variations (Fig. 109). Wolf predation is a major culling force that has shaped

survival patterns, behavior, and physical characteristics of prey throughout their evolutionary history, resulting in prey that are well-adapted to their environment. On Isle Royale, as predation intensified with increased prey vulnerability, the degree of control exerted on the moose population probably increased—especially as prereproductive moose became vulnerable. In such a situation wolf predation is not compensatory, as Errington (1946) defined it, since other mortality factors could not fully substitute for predation. Wolves hasten the death of moose that would die eventually of other causes, but the time element is critically important. Intensive culling ensures that limited food resources are utilized by the most vigorous members of the prey population.

The role of predation may be clarified if we consider a hypothetical question: what would happen if wolves were removed from Isle Royale? Malnutrition would take over as the principal direct and indirect source of mortality, affecting mainly calves and old moose in late winter and early spring. In the absence of predation, moose weakened by malnutrition may survive for months, competing with healthy moose for limited browse. Calves would be born weaker and smaller than usual, and neonatal mortality probably would increase. Thereafter calf mortality would be low, with the degree of loss to malnutrition in late winter and spring determined by winter weather. Over a series of mild winters the moose population would increase because of low adult mortality and relatively high calf survival. With the return of usual winter conditions mortality would greatly increase, and severe winters probably would cause large losses. Long-term population levels of moose might well be lower without predation because of wasteful browse utilization. Thus wolves are essential to the maintenance of a healthy, high-density moose population on Isle Royale.

Although wolves did not hold the population on Isle Royale below the level at which food supply and environmental conditions affected the welfare of moose, wolf predation increased during the 1970s when moose, particularly calves and young adults, became unusually vulnerable. As long as wolves and moose coexist on Isle Royale, wolf predation will remain the principal mortality factor operating on the moose herd. However, the degree of control exerted by predation will be determined largely by environmental influences (principally food supply) that act on moose reproduction as well as vulnerability to regulate numbers of moose.

Wolf Population Adjustments

The recent partitioning of Isle Royale into two pack territories is a significant departure from the basic pattern of the 1960s. The remarkable stability shown during the 1960s demonstrated that effective natural controls were operative. The primary regulatory influence was believed to be food supply or social controls, or some combination. Until recently wolf densities on Isle Royale and in other regions were not found to exceed one wolf per 25 km^2 (Pimlott 1967), leading to the inference that this was a maximum density beyond which wolves would not

increase, perhaps because of social intolerance (Huffaker 1970). High pup mortality in other wolf populations has been regarded as important in reducing their growth potential, and the finding of an apparently malnourished pup on Isle Royale in 1964 suggests that food shortages during the pup-rearing season were of regulatory significance (Jordan et al. 1967). However, Wolfe and Allen (1973) found that the wolf population, at a low level in the late 1960s, did not increase immediately following a winter when moose vulnerability was high and surplus killing was evident; they proposed that social factors might be preventing expansion.

The emergence of a second pack of wolves on Isle Royale and the expansion of their population reflects an increased food supply stemming from greater vulnerability of moose and a higher beaver population. Thus, the level of food resources available to Isle Royale wolves is proposed as the principal underlying variable which determines the number of stable packs and, ultimately, wolf population levels.

In some cases "food supply" for predators may be correlated directly with prey densities, and predator populations will fluctuate in direct response to changes in prey levels. This is especially true of predators that are not as selective as wolves, such as lions preying on certain ungulates species (Schaller 1972) and coyotes preying on jackrabbits (Clark 1972). More selective predators, such as Isle Royale wolves, are particularly apt to respond to changes in numbers of vulnerable moose, rather than prey densities per se. In this context the relationship of moose welfare to environmental influences is critical in understanding wolf population responses on Isle Royale.

At the pack level, food plays an obvious role in regulating group size, since wolf-pack size is related to the size of their prey. Packs feeding on Isle Royale moose have numbered between 15 and 20 wolves, those feeding on elk (*Cervus canadensis*) and mule deer (*Odocoileus hemionus*) contained between 6 and 14 members (Carbyn 1974a, b), and wolf packs feeding only on deer usually numbered 7 or less (Mech 1973; Van Ballenberghe 1972). Food level can affect wolf populations directly, particularly through pup mortality and survival (Van Ballenberghe and Mech 1975, Seal et al. 1975). In addition, the complex social organization found within and between wolf packs may provide for subtle influences on physiology and behavior that may be of regulatory importance.

Territoriality among wolf packs apparently is a spacing mechanism which adjusts wolf densities to their food level. This explains the recent reorganization of the Isle Royale wolf population. In response to increased food resources, the single resident pack ranged in winter over only half of the island in 1971, and the second pack became established the following year on the remaining half. Without a shrinkage in the original pack's territory, a second pack could not have materialized. Similarly the increased size of the winter territory of the East Pack in the first 3 years of its existence was correlated with a decrease in the amount of food

available to each pack member in winter. This led to considerable spatial overlap and, in at least one case, direct mortality from inter-pack aggression.

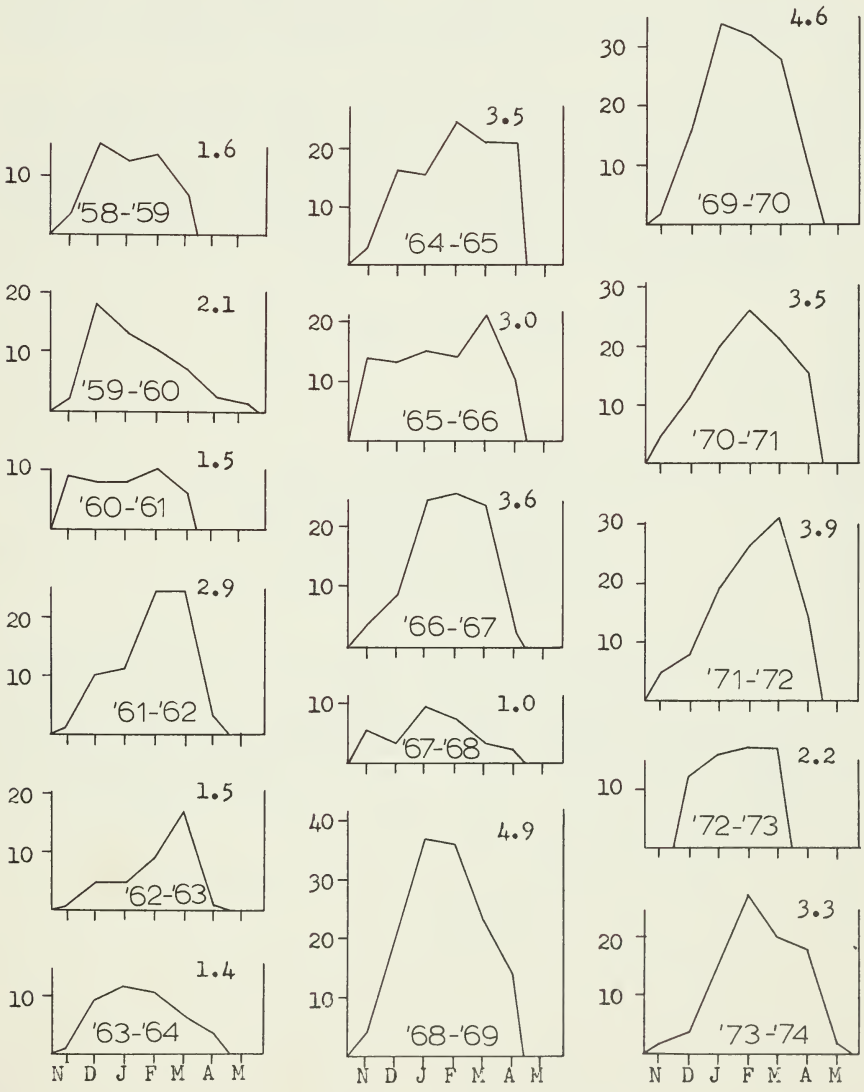
Social relationships within the pack may also be sensitive to food supply and thus influence pack size. Social stress, particularly for subordinate wolves, probably increases when food is short. The physiology of individual wolves may be affected by social interaction—perhaps affecting their reproductive capabilities. Social restraints seem to reduce the incidence of breeding among adults in a pack. Dispersal of young wolves may sometimes have significance. At present we do not really understand all these possible mechanisms nor their relative effectiveness.

Environmental conditions certainly influence predator populations—sometimes directly. In northern areas climatic factors may contribute to regulation of predator numbers by increasing the energy costs of body maintenance and normal activities. Pup survival may sometimes be affected (Clark 1971).

Natural regulation of a predator population appears to result from a complex of factors: food supply as the underlying principal variable, mediated by social and/or environmental influences. The nature and relative influence of these factors probably will vary considerably depending on the predator and prey species involved and the environmental conditions which render each interaction unique.

APPENDIX A

Maximum snow depths recorded at Grand Marais, Minnesota (USDC 1958-74). A snow-depth index (upper right of each graph) was calculated for each year by determining the area under the curve. Vertical axis is snow depth (inches), horizontal axis is the month of the year.



APPENDIX B

Notes on snow-analysis equipment and procedure.

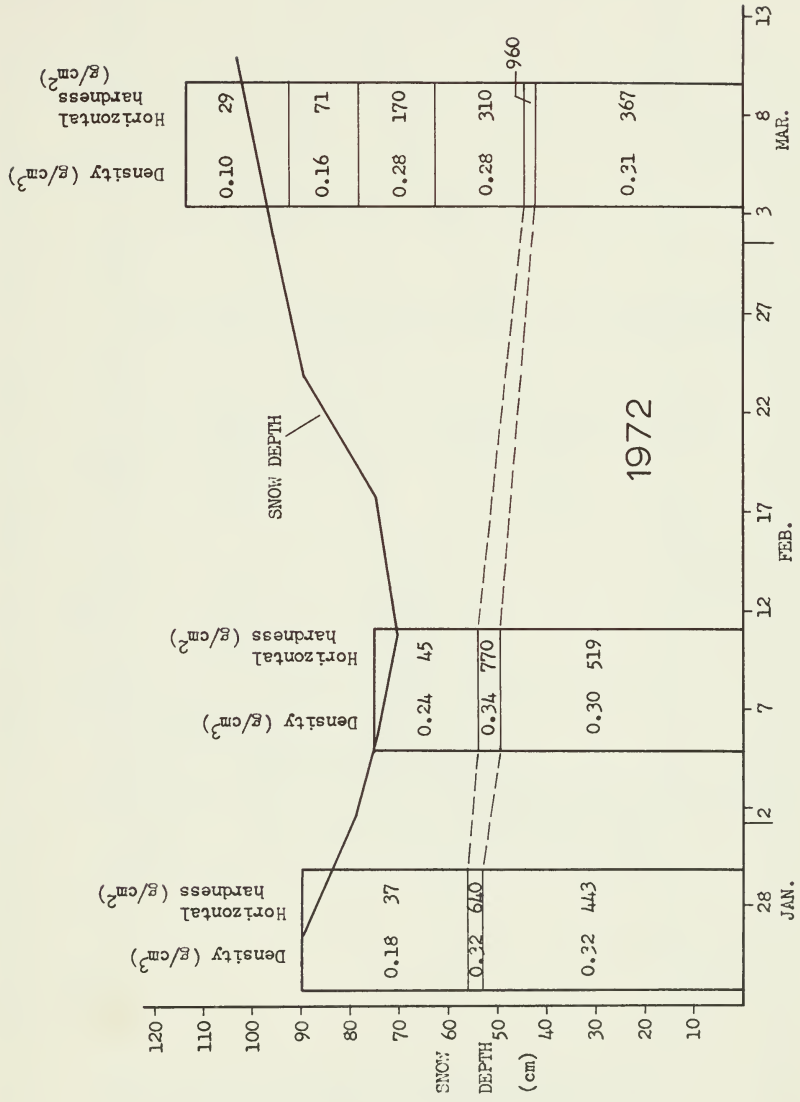
1. In 1972 and 1973 a compaction gauge similar to that described by Verme (1968) was used. The compaction gauge (cross-sectional area: 1.98 cm^2) could be loaded with lead weights to simulate any load up to 650 g/cm^2. The general procedure was to begin at 100 g/cm^2, and increase the weight load until the instrument reached the ground when dropped from the snow surface. Because of the great variability in snow cover, 10 or more readings were taken for each weight load, at increments of 50 g/cm^2.

2. In 1974 a Rammsonde (Ram) penetrometer replaced the compaction gauge as the preferred instrument with which to measure the support quality of the snow. This consists of a stainless steel rod tipped with a 120° cone, 10 cm in diameter. A 1-kg drop hammer was dropped from a given height (30 cm was used) along a guide rod, forcing the Ram into the snowpack. The depth after each blow was recorded, until the tip penetrated to within 3 cm of the ground surface. The Ram hardness number was computed from the following expression (*Testlab* 1970; Coady 1974a):

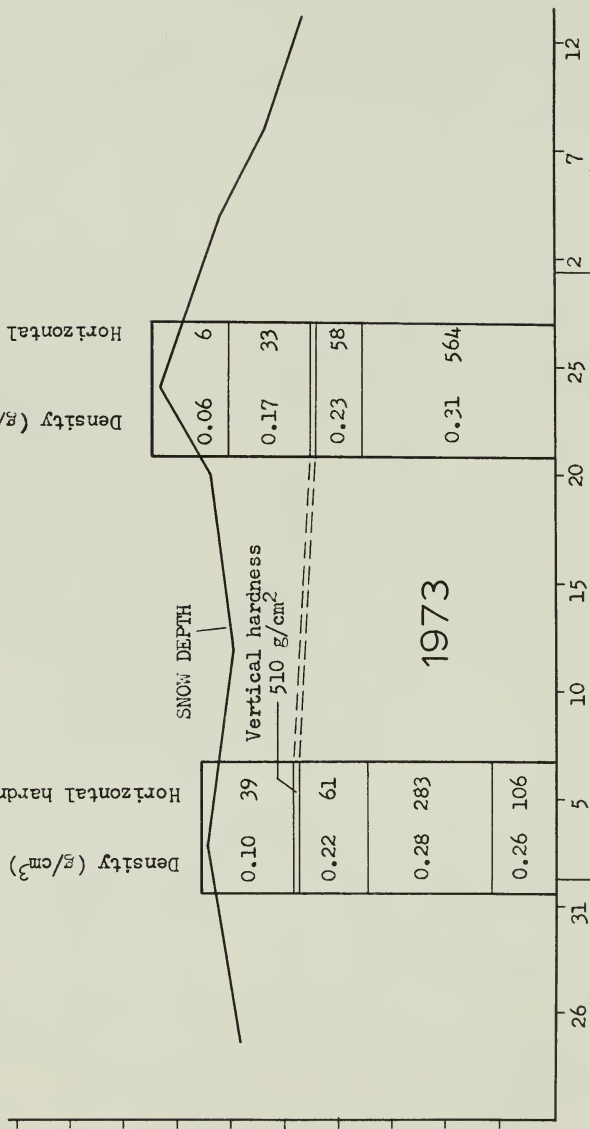
$$10R = \frac{Whn}{x} + W + Q, \text{ where}$$

R = Ram hardness drop
W = weight of drop hammer (kg)
h = height of drop (cm)
n = number of hammer blows
x = penetration after n blows (cm)
Q = weight of penetrometer (kg)

3. Density of snow was determined by weighing 500 ml of snow extracted from the snow profile with a *Testlab* snow cutter. Show hardness was measured with a Chatillon "Push-Pull" gauge fitted with circular plates measuring 1, 10, or 100 cm^2 in area. The gauge measured up to 1000 *g* of force, and a sliding disc measured the greatest force obtained on a single trial. The plates were placed flat against the snow surface to be tested and a force applied until the snow structure collapsed, as described by Klein et al. (1950).



Snow-profile analyses in an open area at Windigo, Isle Royale National Park during the winter study period, 1972.



Snow-profile analyses in an open area at Windigo, Isle Royale National Park, during the winter study period, 1973.

Snow-profile analysis in an open area at Windigo, Isle Royale National Park, during the winter study period, 1974.

APPENDIX D

Dates and extent of field work on Isle Royale, 1970–74.

Year	Dates	No. weeks	Distance Hiked (km)		Hours flown (winter)
			On trails	Off trails	
1970	14 June–27 Aug.	10	628	81	–
1971	26 Jan.–11 Mar.	7	–	–	99
1971	8 June–7 Sept.	13	612	362	–
1972	23 Jan.–10 Mar.	7	–	–	92
1972	9 May–1 Nov.	25	857	657	–
1973	24 Jan.–16 Mar.	7	–	–	87
1973	4 May–10 Nov.	27	869	906	–
1974	23 Jan.–17 Mar.	7	–	–	98
	Totals	103	2966	2006	376 + 30 hr fall moose survey

APPENDIX E

Whole weights of Isle Royale moose in winter

Autopsy No.	Date of collection	Sex	Age	Weight (kg)
818[a]	27 Jan. 1973	F	8 mo	186
447	21 Feb. 1969	M	9 mo	136
643	15 Feb. 1972	F	5.5 yr	400
817[a]	27 Jan. 1973	F	7.5 yr	363
644	21 Feb. 1972	M	6.5 yr	449
537	4 Feb. 1971	M	7.5 yr	431
504	8 Feb. 1970	M	7.5 yr	425

[a]817 and 818 were a cow and its calf.

APPENDIX F

Description of sexual behavior, excluding actual copulation, observed among Isle Royale wolves. Number of times observed in parentheses.

Mounting (14). A wolf approaches from behind and clasps its partner around the midsection with its front legs immediately in front of the partner's hind legs. Although females at Brookfield occasionally mounted males in similar fashion, I have not confirmed this on Isle Royale. Among the alpha pairs, females were never observed mounting males. This is, of course, a preliminary to actual copulation.

Riding up (3). A wolf places both front feet on the back or rump of a conspecific and raises itself up, sometimes straightening its front legs. Both sexes showed this behavior during courtship, and it frequently precedes mounting of females by males. Preliminary to mounting, the wolf places its front paws on the back of its partner in a riding-up movement, then moves its front feet toward the rear of its partner, finally clasping the partner as in mounting.

Play-soliciting (11). Identical to behavior of a playful dog. The play-soliciting wolf shows exaggerated ambivalent approach-withdrawal behavior, running up to its partner and lowering its forequarters to the ground, then jerks its head to one side and runs off, inviting chase. Usually the ears of such an animal are somewhat flattened, and often a "play face" or "play grin" is exhibited, in which the mouth is open and the tongue hangs out, as in panting. This is often followed by typical play behavior, with much nipping and biting about the scruff of the neck, wrestling with interlocked front legs, and "jaw-wrestling" with open mouths.

Chinning (2). The underside of the lower jaw is placed on the back, scruff, or rump of another animal, while usually standing perpendicular to the other animal.

Genital examination (17). This was the most common form of courtship behavior recorded in the study. A male approaches a female and sniffs and examines her genital area, sometimes licking. The odor of a female in estrus is very characteristic and noticeably stimulates male sexual behavior (Schenkel 1947). Genital examination is possible only if there is mutual response in the female, in which case the female averts her tail.

Greeting (12). Elements of greeting behavior, when seen in conjunction with other courtship behavior, were considered to be an integral part of the pair-bond formation and maintenance. Tail-wagging, muzzle-licking, and nose-to-nose contact was most common and often occurred during play between a bonded male and female. This type of greeting behavior is similar to active submission.

Body contact (3). When traveling, a pair often trotted side-by-side, with frequent contact. Body "slams" against the hip and shoulder are occasionally observed during play between mates. When the pack rests, a mated pair will usually lie down next to each other, although this was not tallied as courtship behavior.

Pawing (3). This was infrequently seen and usually functioned as an attention-getting device when the mate being pawed was resting or engaged in other activity, such as feeding.

APPENDIX G

Summary of foxes seen in winter on Isle Royale.

	1972	1973	1974
Moose carcasses located	38	30	40
Utilized by foxes[a]	23 (61%)	14 (47%)	26 (65%)
Foxes on utilized carcasses			
Average maximum number	2.4	1.3	1.9
Sum of max. numbers	55	18	48
Other fox observations[b] per 100 hours flying	25	24	21

[a]Foxes observed at carcass.

[b]Foxes seen from the air more than 0.8 km from a known carcass.

APPENDIX H

Formulas used to calculate stratum variance and confidence intervals for aerial moose censuses (from Wolfe and Jordan, unpubl. data).

Individual stratum variance (s_i^2) was calculated in the following manner:

$$s_i^2 = \left[\sum_j \left\{[(m_{ij}/a_{ij}) - \bar{m}_i]^2 (a_{ij})\right\} \Big/ (n_i - 1)(\Sigma a_{ij})\right](1 - P_i)$$

where:

m_{ij} = number of moose in jth plot of the ith stratum.
a_{ij} = area (mile^2) of the jth plot of the ith stratum.
$\bar{m}_i$ = mean density (moose/mile^2) of the ith stratum.
n_i = number of plots sampled in the ith stratum.
P_i = proportion of total area of the jth stratum sample.

Standard error of the mean density for the island:

$s_{\bar{m}} = \sqrt{\sum_i (A_i^2 s_i^2)}$, where A_i and s_i^2 are the areas and variances, respectively, of the individual strata.

95% confidence interval for population estimate of the island (X):

Estimate ± 95% confidence interval = $X \pm t_{0.05}(s_{\bar{m}})$, where $t_{0.05}$ is the Student's "t" statistic with n_i degrees of freedom.

APPENDIX I

Distance from shorelines[a] of kills of calf and adult moose in midwinter.[b]

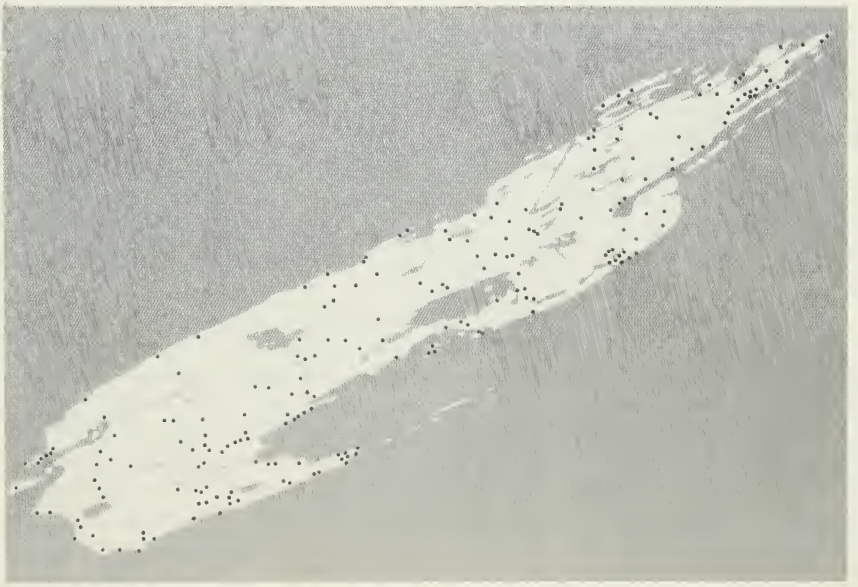
Distance from shore	Calves		Adults	
	No.	%	No.	%
Less than 50 m	42	39.3	53	24.3
50–200 m	21	19.6	32	14.7
200–400 m	11	10.3	32	14.7
400–800 m	9	8.4	23	10.6
800–1600 m	7	6.5	21	9.6
Greater than 1600 m	17	15.9	57	26.1
Total	107	100.0	218	100.0

[a]Lake Superior or Siskiwit Lake.

[b]Contingency table analysis indicates a significant difference ($\chi^2 = 11.93$, 5 d.f., $P < 0.05$).

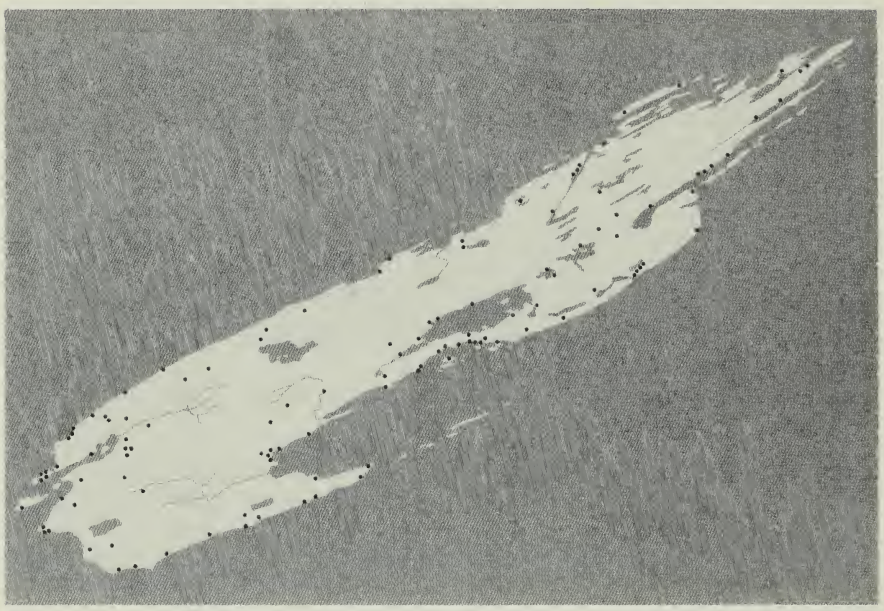
APPENDIX J

Distribution of 218 adult moose killed by wolves in midwinter, 1959-74



APPENDIX K

Distribution of 107 calf moose killed by wolves in midwinter, 1959-74.



1975 and 1976. The Isle Royale wolf population continued to increase in 1975 and 1976, following the trend detailed above. In February 1975 the island supported 41 wolves, and we witnessed the establishment of a third pack, the Middle Pack, between the East and West packs. The Middle Pack appeared to consist of an adult pair and five pups. The East Pack reached a peak of 18 wolves, while the West Pack dropped slightly to 10 members. A trio and a loner also were found at the southwest end of the island, and there was a duo in the middle.

In 1976 the winter wolf population totaled 44, broken down as follows: 17 in the East Pack, 9 in the West Pack, 4 in the Middle Pack and an adjacent group of 3 that probably had split off this pack, plus additional groups of 4, 3, and 2, and 2 loners. In February the West Pack attacked the pack of 4 wolves within their territory and killed two of them.

Established trends in the moose population continued: calf production and survival were low, and predation increased as the wolf population continued to grow. In contrast to the early 1970s, wolves again began to prey intensively only on calves and old adult moose. Details of the wolf population and wolf-moose relationships in the post-1974 period will be published at a later date.

Age distribution of wolf-killed moose found during winter study on Isle Royale, 1959–74.

Age (yrs)	1959	'60	'61	'62	'63	'64	'65	'66	'67	'68	'69	'70	'71	'72	'73	'74[a]	Total	%
calf	4	10	4	2	2	6	3	4	1	2	13	7	19	17	7	10	111	33.8
1–2	–	–	–	–	–	2	2	2	–	1	2	3	–	4	4	1	21	6.4
2–3	–	–	–	–	–	–	–	–	–	1	–	–	2	4	5	–	12	3.7
3–4	–	–	–	1	–	–	–	3	–	–	–	1	3	1	3	–	12	3.7
4–5	1	–	–	–	–	–	–	1	–	–	–	–	1	–	1	1	5	1.5
5–6	–	–	–	–	–	–	–	–	1	–	–	–	–	1	–	1	3	0.9
6–7	1	2	3	1	–	–	1	1	–	1	–	–	1	2	1	–	14	4.3
7–8	2	3	1	1	–	–	–	–	–	–	2	–	2	1	1	1	14	4.3
8–9	1	1	2	1	1	–	–	–	1	1	3	1	3	1	–	–	16	4.9
9–10	–	1	3	3	3	3	1	–	–	–	–	–	–	2	1	2	16	4.9
10–11	2	–	2	2	4	2	–	1	–	1	2	–	–	–	1	–	18	5.5
11–12	–	–	1	2	2	5	4	1	1	1	1	–	–	1	2	1	19	5.8
12–13	–	–	4	2	2	–	2	2	2	–	–	–	–	–	–	1	20	6.1
13–14	–	1	2	–	2	–	2	1	1	2	1	1	–	–	1	–	14	4.3
14–15	–	–	–	–	–	–	2	1	3	–	1	1	–	–	–	–	8	2.4
15–16	–	–	–	–	–	–	2	–	–	1	–	–	–	1	–	1	5	1.5
16–17	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	0.3
17–18	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	1	0.3
18–19	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
19–20	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Unk. age adult	2	–	4	–	–	–	3	4	–	–	–	–	1	1	2	1	18	3.5
Total	13	18	26	15	16	18	22	21	10	11	26	14	32	36	29	21	328	
% calves	31	56	15	13	12	33	14	19	10	18	50	50	59	47	24	48		

[a]Partial listing only.

APPENDIX M

Sex and age distribution of 482 adult moose skeletal remains and approximate time of death. These data were used to construct the life table presented in Table 35.[a]

Age (yrs)	Period of Death (sorted according to sex)																				
	1950–54			1955–59			1960–64			1965–69			1970–74			Total				
	♂	♀	Unk	♂	♀	Unk	♂	♀	Unk	♂	♀	Unk	♂	♀	Unk	♂	♀	Unk		
1–2	3	–	–	–	–	–	3	–	–	8	3	2	11	12	1	25	15	3		
2–3	–	–	–	–	–	1	1	2	–	4	3	–	10	5	–	15	10	1		
3–4	1	–	2	–	–	–	3	1	2	3	3	1	6	8	–	13	12	5		
4–5	2	1	–	–	2	–	2	2	1	2	–	1	5	4	–	11	9	2		
5–6	4	1	1	2	3	1	1	–	1	3	1	–	2	2	–	12	7	3		
6–7	1	1	–	1	–	–	1	9	1	4	3	–	5	8	1	12	21	2		
7–8	1	–	–	–	2	1	7	3	3	5	2	–	8	5	–	21	12	4		
8–9	4	3	1	1	–	2	6	4	–	6	4	–	6	3	1	23	14	4		
9–10	2	1	2	2	2	–	9	7	1	2	2	–	6	6	1	21	18	4		
10–11	1	–	4	1	3	1	11	8	1	1	8	1	6	–	–	20	19	7		
11–12	–	–	–	1	–	–	9	8	–	7	5	1	8	7	1	25	20	2		
12–13	–	–	–	–	–	1	7	11	–	2	8	–	3	4	–	12	23	1		
13–14	–	–	–	1	–	–	3	4	–	8	6	–	2	4	–	14	14	–		
14–15	–	–	1	–	–	–	1	–	–	3	5	–	2	1	1	6	6	2		
15–16	–	–	–	–	–	–	–	–	–	2	1	1	1	2	–	3	3	1		
16–17	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	2	–		
17–18	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	2	–		
18–19	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–		
19–20	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	1	–		
Total	19	7	11	9	12	7	64	59	10	60	56	7	81	74	5	233	208	41		

[a]Included in the life-table calculations are 54 additional carcasses which could not be assigned to a 5-year period of death.

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